Population and community ecology and ecosystem ecology provide two different perspectives on ecological systems, their structure, their functioning, their dynamics and their evolution. While population and community ecology takes as its starting point the population and its interactions with other populations, ecosystem ecology is mainly concerned with the flows of matter and energy in the overall system composed of biological organisms and their abiotic environment.

Linking Community and Ecosystem Ecology (LINKECOL)

An ESF scientific programme

However, populations and communities do not exist in isolation; they are parts of ecosystems, and, as such, they are subjected to constraints arising from ecosystem functioning, in particular energy dissipation and nutrient cycling. At the same time, ecosystems do not exist without their biological components; the latter impose their own constraints on ecosystem processes, as the disruptions generated by some biological invasions attest. And in the face of the growing threat of a massive loss of biological diversity, interest is increasing concerning the role of biodiversity in ecosystem processes.

This has created an urgent need to integrate the two subdisciplines and it is the principal aim of the LINKECOL programme to unify these different perspectives. Such integration is essential not only to advance our fundamental understanding of natural and managed ecosystems but also to provide answers to more applied questions such as the impacts of biodiversity loss or species invasions on ecosystem sustainability.

The European Science Foundation acts as a catalyst for the development of science by bringing together leading scientists and funding agencies to debate, plan and implement pan-European initiatives.

Scientific background

The need for integration of population/community and ecosystem ecology

The vigorous growth in ecology from its origins in the early years of the 20th century has been accompanied by the creation of numerous subdisciplines. Although specialisation may be inevitable, it also creates problems because conceptual frameworks in different subdisciplines often diverge over time. This is nowhere more apparent than between two of the major subdisciplines of ecology: population and community ecology on the one hand and ecosystem ecology on the other. These two subdisciplines have grown largely independently, each having its own concepts, theories and methodologies. Population and community ecology is mainly concerned with the dynamics, evolution, diversity and complexity of the biological components of ecosystems; its starting point is the population and its interactions with other populations. Ecosystem ecology is mainly concerned with the functioning of the overall system composed of biological organisms and their abiotic environment; its starting point is the flow of matter or energy among functional compartments.

This separation of the two subdisciplines is understandable as they partly address issues at different hierarchical levels and different spatial and temporal scales. But it is harmful insofar as it is an obstacle to their unity and mutual enrichment. Populations and communities do not exist in isolation; they are parts of ecosystems, and, as such, they are subjected to constraints arising from ecosystem functioning, in particular energy dissipation and nutrient cycling. These constraints can deeply alter the nature of species interactions and community properties such as food-web stability. On the other hand, ecosystems do not exist without their biological components; the latter impose their own constraints on ecosystem processes, as the disruptions generated by some biological invasions attest. In the face of the growing threat of a massive loss of biological diversity, interest is increasing concerning the role of biodiversity in ecosystem processes. There is today an urgent need for integration of the two subdisciplines.

Such an integration is already emerging on a world-wide scale as well as in Europe, as a result of both basic and applied scientific questions: How will changes in species and genetic diversity affect ecosystem processes and the related services they provide to humankind? How will these changes affect the stability of ecosystems, and their ability to withstand natural and anthropogenic perturbations? How do biological organisms and abiotic factors interact to regulate the flow of energy, the structure of the food web and the cycling of chemical elements in aquatic and terrestrial ecosystems? On a large time scale, are plants, animals and micro-organisms involved in mutualistic relationships mediated by material cycling despite their apparent immediate antagonism? Can

indirect interactions evolve by natural selection and significantly influence species traits? These are some examples of the questions that have recently received growing attention.

Both population, community and ecosystem ecology have a long history in Europe, but, as mentioned above, these subdisciplines have had largely separate developments, with different strengths in different countries and laboratories. Attempts towards the goal of integration of the subdisciplines are developing rapidly through new experimental and theoretical approaches, but they are still dispersed, both scientifically and geographically. European ecology would greatly benefit from a co-ordinated effort to stimulate exchanges of ideas, of new theoretical insights, of new experimental systems, and of researchers among European countries.

The effects of plant species diversity on ecosystem processes are investigated using field experiments in European grasslands.
© N. Buchmann

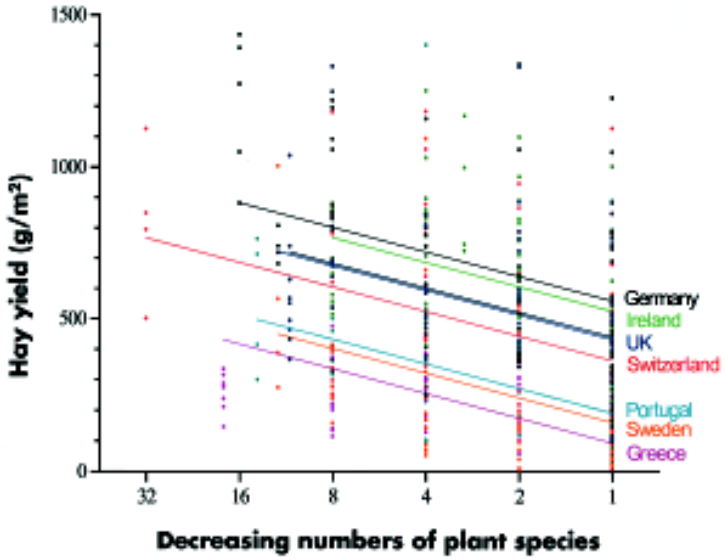
The ESF programme

The present programme aims at unifying the perspectives of community and ecosystems ecology. This is an important scientific challenge, both to improve our fundamental understanding of natural and managed ecosystems and to provide appropriate answers to more applied questions such as the impacts of biodiversity loss or species invasions on ecosystem sustainability. The goal of the programme is to promote the development and integration of research linking community and ecosystem ecology across Europe. The programme will strengthen interactions among groups from different countries and different scientific traditions, stimulate the development of ideas, support the initiation of collaborative research projects, facilitate the exchange of knowledge and expertise, and attract new groups and researchers to the field. It will also provide a European contribution to the *Diversitas* and IGBP-GCTE international programmes. The programme will be centred on the three main scientific themes:

1. Species diversity and ecosystem processes;
2. Ecology and evolution of indirect effects in ecosystems;
3. Biological invasions and ecosystem processes.

1. Species diversity and ecosystem processes

Until recently little attention has been given to the ecological consequences of the losses of biodiversity. Most concerns over biodiversity losses have focused on the important ethical and aesthetic dimensions of biotic impoverishment or on the losses of potentially economically valuable crops or drugs. There is now growing recognition, however, that ecosystems operate in a manner that provides free ecological services to humans. These services are derived from the normal functioning of ecosystems, raising the important question whether depauperate ecosystems perform differently or less efficiently than the more species-rich systems from which they are derived.



The loss of plant species diversity reduces primary production in European grasslands (Hector et al., Science 286:1123-1127, 1999).

Several hypotheses have been proposed on this topic, ranging from one extreme stating that all species are unique in their contribution to ecosystem performance to the other extreme stating that most species in a functional group are redundant in their ecosystem impact. Another possibility is the "insurance hypothesis" : High species richness may not always play a significant role in maintaining ecosystem processes under constant or benign environmental conditions, but it may nevertheless be important for maintaining their stability under changing environmental conditions.

Global or more local environmental changes such as increased atmospheric CO_2 concentration or N deposition are likely to interact with changes in biodiversity and ecosystem processes. These environmental changes may have profound effects on ecosystem processes such as productivity, soil acidification and nutrient mineralisation, which affect the competitive balance between plant species and result in changes in species diversity and composition. These changes in species diversity and composition in turn may have important impacts on soil organic matter dynamics and nutrient cycling, thus affecting ecosystem functioning.

This part of LINKECOL has the following aims:

- To synthesise current experimental and theoretical advances in the area of the effect of biodiversity on the magnitude and stability of ecosystem processes.
- To develop innovative approaches in this area.
- To contribute to an understanding of the mechanistic basis of the response – or lack of response – of ecosystem processes to species diversity.
- To investigate the functional properties, at the aggregated ecosystem level, of mechanistic theories of interspecific competition and coexistence based on resource consumption, space occupancy or response to disturbances.
- To investigate, both theoretically and experimentally, the interplay between ecosystem processes and community assembly.
- To examine how environmental changes interact with changes in biological diversity in determining ecosystem processes.

2. Ecology and evolution of indirect effects in ecosystems

Interactions between organisms and between organisms and their abiotic environment are not only direct, but they also have a great number of indirect effects on other organisms and processes. Some of these indirect effects have a considerable impact on the functioning of ecosystems. Well-known examples are keystone predation, indirect mutualisms between plants and predators, or indirect facilitation by ecosystem engineers.

Reciprocally, some ecosystem processes mediate significant indirect effects among organisms and thereby modify the nature of species interactions. In particular, nutrient cycling plays a crucial role as a circular causal pathway which transmits indirect effects to all ecosystem components. A clear if controversial example of this is to be found in plant—herbivore interactions. While the direct trophic interaction between plants and herbivores is negative for the plants, the positive indirect effect of herbivory due to increased nutrient cycling by the herbivores may result in a net gain in productivity for the plants, thus generating an indirect mutualism between plants and herbivores. Another example concerns indirect effects generated by differential recycling of mineral elements due to differences in elemental constraints (C/N/P ratios) among trophic levels.

Many indirect effects in ecosystems are still poorly understood, both theoretically and experimentally. Yet they may be critical for our understanding of the long-term impact of species losses. Their evolutionary implications may also be considerable, but the evolution of indirect interactions is an area of evolutionary biology that poses complex problems and is only starting to receive some attention. Research into this area may well drastically change our understanding of the evolution of species under natural conditions.

Some aims of this sub-programme are:

- To identify indirect effects generated by species interactions that have a consistently significant impact on ecosystem processes.
- To develop new theories and experiments on indirect effects mediated by material cycling or other ecosystem processes.
- To understand the relationship between the spatial scale considered, the spatial heterogeneity of the environment and species interactions, and the extent and magnitude of indirect effects.
- To develop new theories and experiments on the evolutionary significance of indirect effects in ecosystems.

3. Biological invasions and ecosystem processes

There has recently been increased attention on the magnitude and impact of biological invasions. Alien invasive species represent a serious problem internationally affecting health, agricultural potential, biodiversity, and the structure and functioning of natural ecosystems. This problem will probably become more acute with increasing global trade, global environmental change and changing land use patterns.

The ecological and economic consequences of invasives are considerable. Biological invasions by exotic species clearly alter the composition and community structure of invaded areas. They often lead to irreversible species extinctions. As a matter of fact, invasive species are considered to be the second greatest threat to biodiversity globally (habitat destruction being the first). They can result in enormous short-term economic losses within managed ecosystems (crops, in particular). Their control

Mesocosm experiments show the importance of indirect effects in the response of lake ecosystems to pertubations such as nutrient enrichment in France. © Lacroix

using chemicals or physical measures often has environmentally damaging consequences, with longer-term economic impacts.

There is increasing evidence that invading species can alter properties of whole ecosystems, including productivity, nutrient cycling, and soil fertility. For example, a predaceous flatworm from New Zealand is currently spreading in Scotland and Ireland. It preys preferentially on earthworms, thus indirectly threatening soil structure and fertility, decomposition processes, and bird communities. Exotic grasses that have invaded semi-arid shrublands and woodlands have increased the probability and severity of fires in many areas.

We still have limited understanding of what makes species successful potential invaders, what increases the resistance of communities or ecosystems to invasions, and what impacts biological invasions have on communities and ecosystems. Such an understanding would allow us to predict when and where biological invasions are more likely to occur, and what their ecological consequences are likely to be. In addition, invasive species provide a good model for integrating ecophysiology, population biology, community ecology and ecosystem ecology. They can reveal the ecosystem impact of individual species, as well as their indirect effects on other species and community processes.

Primary aims of this part of LINKECOL are:

- To identify the ecological attributes of invasive species that contribute to the success or failure of their invasion in an ecosystem.
- To investigate, theoretically and experimentally, the properties of communities and ecosystems that make them more resistant or resilient to invasions.
- To develop comparative investigations of the population ecology of invasive organisms in their native and exotic areas, and identify research protocols for such investigations.
- To develop the ability to predict the community and ecosystem impacts of biological invasions.

Activities

Workshops

The programme will fund workshops dealing with aspects of the scientific themes. Some workshop themes will be suggested by the steering committee, but there will also be funding available for other workshops on themes suggested by individuals in the participating countries. Calls for proposals for workshops will be made annually (October 1999, March 2000). In 2000 two workshops are scheduled:

- Elemental constraints on energy transfer in food webs
- Biodiversity and ecosystem functioning

Workshops will be attended by about 40—50 scientists with a significant proportion of young researchers. They will be open to researchers from all European countries. The Scientific Steering Committee will also promote smaller workshops on newly emerging research topics.

Exchange visits

The exchange visits scheme will support working visits of up to 6 months by young or leading researchers visiting laboratories outside their home country to work on collaborative research on one of the research themes of the programme. Exchange visits are important to increase mobility between European centres, promote the coherence of research in Europe, and bring together experts with complementary skills from different countries.

Applications will be granted on the basis of letters of reference, past performance, quality of the project proposal and compatibility with the scientific themes of the programme. Details are available on the programme's web site *(http://www.esf.org/linkecol)*.

The functional significance of forest species diversity is explored with a canopy crane in Switzerland. © C. Körner

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For the latest information on this programme consult the *LINKECOL* home page: http://www.esf.org/linkecol

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