Ajith H. Perera · Urmas Peterson
Guillermo Martínez Pastur
Louis R. Iverson *Editors*

Ecosystem Services from Forest Landscapes

Broadscale Considerations

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Editors
Ajith H. Perera
Ontario Forest Research Institute
Ministry of Natural Resources and Forestry
Sault Ste. Marie, ON, Canada

Urmas Peterson
Institute of Forestry and Rural Engineering
Estonian University of Life Sciences
Tartu, Estonia

Guillermo Martínez Pastur
Centro Austral de Investigaciones
Científicas (CADIC)
Consejo Nacional de Investigaciones
Científicas y Técnicas (CONICET)
Ushuaia, Tierra del Fuego, Argentina

Louis R. Iverson
Northern Institute of Applied Climate
Science
Northern Research Station
US Forest Service
Delaware, OH, USA

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Preface

Over the last two decades, the topic of ecosystem services has attracted the attention of researchers, land managers, and policy makers around the globe. The ecosystems addressed thus include an array of aquatic and terrestrial systems including oceans, lakes, rivers, wetlands, grasslands, forests, croplands, and urban areas. The services rendered by these ecosystems are also a long list, ranging from intrinsic to anthropocentric benefits that are typically grouped as provisioning, regulating, supporting, and cultural. The research efforts, assessments, and attempts to manage ecosystems for their sustained services are now widely published in scientific literature.

Nearly 200 researchers gathered in Tartu, Estonia, from August 23 to 30, 2015, under the sponsorship of the IUFRO working party on landscape ecology to discuss the topic "sustaining ecosystem services from forest landscapes." A major theme that emerged from the proceedings was the necessity to broaden the scope of land use planning through adopting a landscape-scale approach. Even though this approach is complex and involves multiple ecological, social, cultural, economic, and political dimensions, the landscape perspective appears to offer the best opportunity for a sustained provision of forest ecosystem services.

This book is a compilation of keynote presentations and syntheses of symposia of the Tartu meeting, focusing on broadscale aspects of forest ecosystem services, beyond individual stands to large landscapes. In doing so, our goal is to create an awareness of the conceptual and practical opportunities as well as challenges involved with planning for forest ecosystem services across landscapes, regions, and nations. However, we must remind the reader that our goal here is not to offer an exhaustive literature review or a comprehensive assessment of the state of knowledge in forest ecosystem services. For that purpose, many general reviews and syntheses can be easily found in scientific literature.

This volume is composed of nine chapters. It begins with a brief introduction to ecosystem services from forest landscapes to provide a topical overview and describe the terminology. The next two chapters draw attention to two relatively lesser known regulatory services from forest ecosystems that have broadscale connotations.

Chapters "Towards Functional Green Infrastructure in the Baltic Sea Region: Knowledge Production and Learning Across Borders", "Sustainable Planning for Peri-urban Landscapes" and "Barriers and Bridges for Landscape Stewardship and Knowledge Production to Sustain Functional Green Infrastructures" address the complexities and multiple issues that are associated with attempts to sustain forest ecosystem services across large landscapes and multiple administrative and political boundaries, whether local or international. Chapters "Solving Conflicts Among Conservation, Economic and Social Objectives in Boreal Production Forest Landscapes: Fennoscandian Perspectives" and "Natural Disturbances and Forest Management: Interacting Patterns on the Landscape" focus on both practical and conceptual aspects deriving ecosystem services from forest landscapes. The concluding chapter summarizes the overall contents and emergent messages of the book and offers some thoughts for future research and applications.

We hope that both developers of scientific knowledge and those who apply that knowledge through policy development and land management will benefit from this discourse. The geographical scope of this book is primarily focused on temperate forest landscapes, and the array of case studies and topics discussed here is by no means globally exhaustive. We anticipate, however, that this volume will offer useful insights to readers in different geographic contexts and also to those who focus on services from non-forested ecosystems. We believe that the various concepts, questions, issues, and solutions presented here, which transcend individual ecosystems and narrower scales around the globe, are valuable contributions to the collective endeavor of expanding our knowledge of this important topic.

Finally, we are indebted to the colleagues who critically reviewed chapter manuscripts and offered suggestions for improvements: Mariano Amoroso, Peter Besseau, Juan Manuel Cellini, Guy Chiasson, Trevor F. Keenan, Timo Kuuluvainen, Lars Laestadius, Silvia Matteucci, Sergio Menéndez, Josep Peñuelas, Chris J. Peterson, Sanna-Riikka Saarela, Andreas Schindlbacher, Ayanda Sigwela, and Susan Smith. Their critiques helped us to greatly improve the veracity and clarity of the messages in this book. We also acknowledge the assistance of Andrea Sandell and Janet Slobodien of Springer New York, who guided us through the publication process.

Sault Ste. Marie, ON, Canada — Ajith H. Perera
Tartu, Estonia — Urmas Peterson
Ushuaia, Argentina — Guillermo Martínez Pastur
Delaware, OH, USA — Louis R. Iverson

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Contributors

Christian Albert Institute of Environmental Planning, Leibniz Universität Hannover, Hannover, Germany

Per Angelstam School for Forest Management, Swedish University of Agricultural Sciences, Skinnskatteberg, Sweden

Endijs Baders Latvian State Forest Research Institute, "Silava", Salaspils, Latvia

Daniel Burgas Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, FL, Finland

Klaus Butterbach-Bahl Institute of Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany

Lucas Dawson Department of Physical Geography and Quaternary Geology, Stockholm University, Stockholm, Sweden

Eugenio Díaz-Pinés Institute of Soil Research, University of Natural Resources and Life Sciences (BOKU), Vienna, Austria

Institute of Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany

Marine Elbakidze School for Forest Management, Swedish University of Agricultural Sciences, Skinnskatteberg, Sweden

Kyle Eyvindson Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, FL, Finland

Lee E. Frelich University of Minnesota, Center for Forest Ecology, Saint Paul, MN, USA

Christine Fürst Institute for Geosciences and Geography, Dept. Sustainable Landscape Development, Martin Luther University Halle, Halle, Germany

Davide Geneletti Department of Civil, Environmental and Mechanical Engineering, University of Trento, Trento, Italy

Aleksandra Grebenzhikova Pskovlesproekt Company, Pskov, Russian Federation

Austra Irbe Zemgale Planning Region Administration, Jelgava, Latvia

Louis R. Iverson Northern Institute of Applied Climate Science, Northern Research Station, US Forest Service, Delaware, OH, USA

Kalev Jõgiste Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Tartu, Estonia

Daniele La Rosa Department Civil Engineering and Architecture, University of Catania, Catania, Italy

Anna Lawrence Scottish School of Forestry, University of the Highlands and Islands, Inverness, UK

Eric Le Tortorec Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, FL, Finland

Liga Liepa Faculty of Forestry, Latvia University of Agriculture, Jelgava, Latvia

Michael Manton Faculty of Forest Science and Ecology, Aleksandras Stulginskis University, Kaunas, Lithuania

Guillermo Martínez Pastur Centro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ushuaia, Tierra del Fuego, Argentina

Viesturs Melecis Institute of Biology, University of Latvia, Salaspils, Latvia

Mikko Mönkkönen Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, FL, Finland

Vladimir Naumov School for Forest Management, Swedish University of Agricultural Sciences, Skinnskatteberg, Sweden

Marharyta Nestsiarenka State Environmental Institution, National Park “Braslavskie Ozera”, Braslav, Belarus

Ülo Niinemets Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia

Kristi Parro Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Tartu, Estonia

Ajith H. Perera Ontario Forest Research Institute, Ontario Ministry of Natural Resources, Sault Ste. Marie, ON, Canada

Urmas Peterson Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Tartu, Estonia

Maiju Peura Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, FL, Finland

Tähti Pohjanmies Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, FL, Finland

Zigmārs Rendenieks Faculty of Geography and Earth Sciences, University of Latvia, Riga, Latvia

Anna Repo Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, FL, Finland

Alena Shushkova SSPA "The Scientific and Practical Center of the National Academy of Sciences of Belarus for Biological Resources", Minsk, Belarus

Marcin Spyra Institute for Geosciences and Geography, Dept. Sustainable Landscape Development, Martin Luther University Halle, Halle, Germany

John A. Stanturf Center for Forest Disturbance Science, Southern Research Station, US Forest Service, Athens, Georgia, USA

Laura Trasūne Faculty of Geography and Earth Sciences, University of Latvia, Riga, Latvia

María Triviño Department of Biological and Environmental Sciences, University of Jyvaskyla, Jyvaskyla, FL, Finland

Siarhei Uhlianets State Scientific Institution, "The Institute of Experimental Botany named after V.F. Kuprevich of the National Academy of Sciences of Belarus", Minsk, Belarus

Uladzimir Ustsin SSPA "The Scientific and Practical Center of the National Academy of Sciences of Belarus for Biological Resources", Minsk, Belarus

Christian Werner Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt, Germany

Maxim Yermokhin State Scientific Institution, "The Institute of Experimental Botany named after V.F. Kuprevich of the National Academy of Sciences of Belarus", Minsk, Belarus

Natalia Yurhenson SSPA "The Scientific and Practical Center of the National Academy of Sciences of Belarus for Biological Resources", Minsk, Belarus

Anton Zhivotov State Scientific Institution, "The Institute of Experimental Botany named after V.F. Kuprevich of the National Academy of Sciences of Belarus", Minsk, Belarus

Ecosystem Services from Forest Landscapes: An Overview

Guillermo Martínez Pastur, Ajith H. Perera, Urmas Peterson, and Louis R. Iverson

1 What are Ecosystem Services?

Human beings derive direct benefit from an array of ecosystem goods as well as from the activities and products of organisms, in both wild and human-dominated ecosystems (Daily et al. 1997; Levin and Lubchenco 2008). These benefits from nature have been readily available throughout most of human history. To this day, societies take many of these natural services for granted (Daily 1997, MEA 2005), even while the support systems that provide them are being severely degraded (Vitousek et al. 1997; Levin and Lubchenco 2008; Seppelt et al. 2011). The central challenge of this century is to develop economic and social systems and supporting systems of governance from local to global scales that will achieve sustainable levels of human population and consumption while also maintaining the ecosystem life-support services that underpin human well-being (Guerry et al. 2015).

The full range of ecosystem benefits to human life is grouped under the concept “ecosystem services” (ES). Since this concept was first introduced (Ehrlich and Mooney 1983), it has evolved (Daily 1997; MEA 2005) into a global phenomenon (e.g., Kubiszewski et al. 2017). ES can be briefly defined as the benefits that humans

G. Martínez Pastur (✉)
Centro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ushuaia, Tierra del Fuego, Argentina
e-mail: gpastur@conicet.gov.ar

A. H. Perera
Ontario Forest Research Institute, Sault Ste. Marie, ON, Canada

U. Peterson
Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Tartu, Estonia

L. R. Iverson
Northern Institute of Applied Climate Science, Northern Research Station, US Forest Service, Delaware, OH, USA

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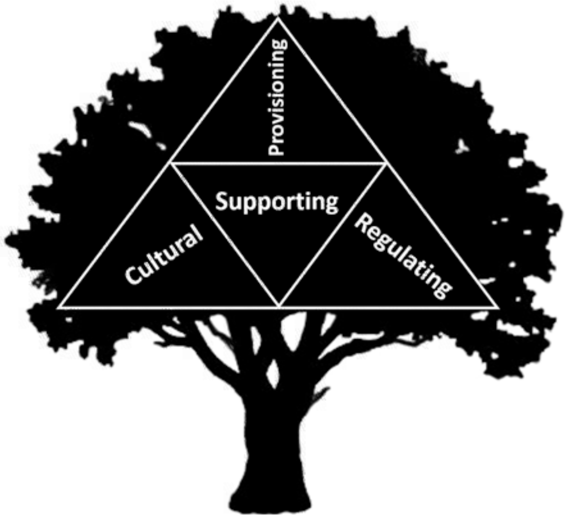

Fig. 1 Four categories of ecosystem services defined by The Millennium Ecosystem Assessment (2005)

obtain from ecological systems (Levin and Lubchenco 2008), consisting of flows of materials, energy, and information from natural capital stocks which, when combined with services derived from human capital to produce human welfare (Costanza et al. 1997). ES comprise ecosystem functions, which refer to the habitat, biological or system properties or processes of ecosystems, and also the ecosystem goods (such as food) and services (such as waste assimilation) which human populations derive, directly or indirectly, from ecosystem functions (Costanza et al. 1997, 2014).

It is possible to recognize four categories of ES (Fig. 1): (i) provisioning services or the provision of food or habitat; (ii) regulating services, such as the regulation of erosion or climate; (iii) supporting services, such as primary production or nutrient cycling; and (iv) cultural services, such as aesthetic enjoyment or recreation (MEA 2005). This classification gave rise to wider understanding of the potential uses of ES and also provided a framework for analyzing the various influences, active and passive, by which ecosystem services enhance human well-being (Boyd and Banzhaf 2007; Fisher et al. 2009). Nevertheless, most of the functions and services included under any one of the four ES categories are interdependent and support human welfare through their contribution to the joint products of the ecosystem (Costanza et al. 1997).

2 What are Forest Landscapes?

Here we define a forest landscape as either a natural or built-up area, at any scale, in which trees dominate the main ecosystems. We include in this definition all of the natural components that are present, together with their spatial heterogeneity, but also the human activities which create and affect patterns and processes within the

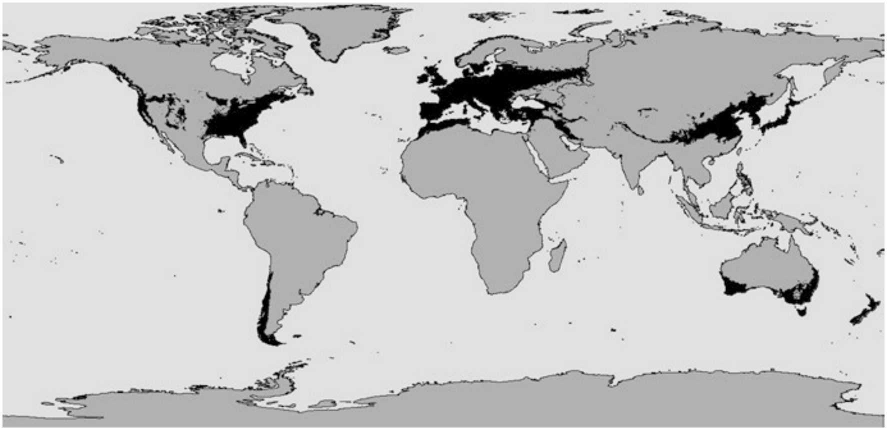

Fig. 2 Distribution of world's temperate forest biome that include broad-leaved, coniferous, and mixed forests (based on www.worldwildlife.org/biomes)

landscape. Forest landscapes cover more than four billion hectares, close to 30% of the Earth's land area, and account for 75% of terrestrial gross primary production and 80% of total plant biomass. They contain more carbon (in biomass and soils) than the total stored in the atmosphere (Beer et al. 2010; Pan et al. 2011). Forest landscapes also harbor most of the species on Earth and provide the most valuable goods and services to humanity (Costanza et al. 1997; Daily et al. 1997).

Temperate forests (Fig. 2), defined here as those forests located between 25° and 55° N and S latitudes, are highly diverse in species and soils and in the carbon pool of their ecosystems (Lal and Lorenz 2012). Temperate forest types vary among broad-leaved evergreen, broad-leaved deciduous, and coniferous, both pure or in combination. These forests are located primarily in the northern hemisphere across all continents but also in southern South America, Africa, and Oceania. Temperate regions of the world have been the most extensively altered by human activities, with significant impacts on the provision of goods and services, as well as the loss of biodiversity (Franklin 1988; Lindenmayer et al. 2012). These forests are the primary focus of our discourse because the need for improved strategies of management and conservation is particularly important there.

3 Ecosystem Services from Forests

The Millennium Ecosystem Assessment (MEA 2005) concluded that since about 1950, 60% of all ES had declined as a direct result of the growth of agriculture, forestry, fisheries, industries, and urban settlement, mainly through the increase in markets for provisioning services, but that similar declines did not occur in the other categories of benefit that ES provide (Kinzig et al. 2011). Forest ecosystems, in

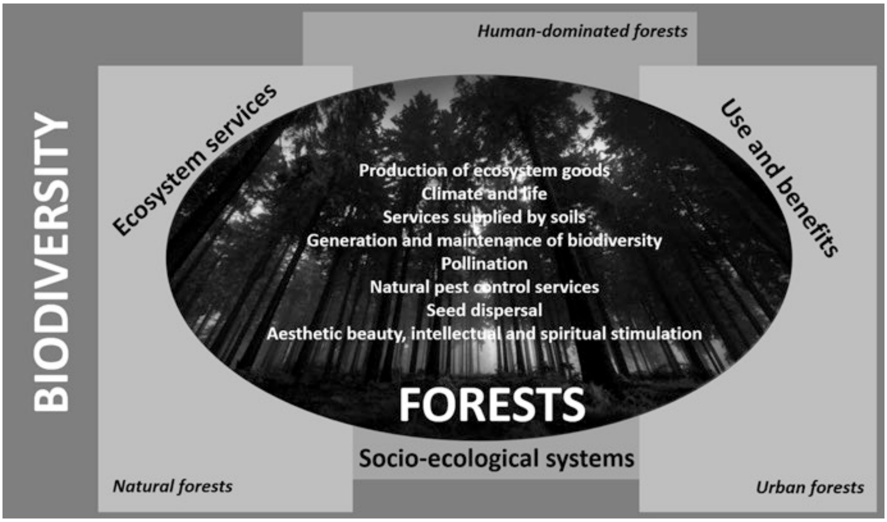

Fig. 3 Importance of forest ecosystem services in natural and anthropogenic landscapes

particular, provide critical ES to humanity (FAO 2010) and harbor most of the global terrestrial biodiversity (Gustafsson et al. 2012). Forests play a multifunctional role in which attempts are made to balance human commodity needs with the production of other goods and services, including the habitat needs of forest-dependent organisms (Thompson et al. 2011; Lindenmayer and Franklin 2002). More than 2 billion hectares of the world's forests (55%) are managed as production forests to supply ES and, at the same time, revenue from timber products to help pay for forest management (Gustafsson et al. 2012; Lindenmayer et al. 2012). When management strategies are developed, however, consideration is seldom given to the full range of ES that forest landscapes provide (Myers 1996; Daily et al. 1997; Nahuelhual et al. 2007) (Fig. 3). Some examples of ES that need to be taken into account are as follows:

- Production of ecosystem goods: The range of products obtained from forests includes food (e.g., fruits, nuts, mushrooms, honey, or spices), fuelwood, fiber, pharmaceuticals, and industrial products (Alamgir et al. 2016; Quintas-Soriano et al. 2016). In addition, animals such as cattle, goats, and sheep are raised in forests' silvopastoral systems (Peri et al. 2016), and these animals are the source of many trade products (e.g., meat, milk, wool, and leather). Hunting is also important in the forests of many countries, both for food and for sport, and can be critical to the survival of low-income people in developing countries (Golden et al. 2014).
- Climate and life: Climate plays a major role in the evolution and distribution of life over the planet, and forests are one of the main factors in the regulation of global climate. Forests help stabilize the climate, lessening extreme events (e.g., by slowing down water runoff) and removing greenhouse gases and other

pollutants from the atmosphere (Beer et al. 2010; Pan et al. 2011; Lal and Lorenz 2012).

- Services supplied by soils: Forests provide a critical role in forming soils, as well as in retaining them through reducing soil erosion. Forest soils moderate the water and carbon cycles, they retain and deliver nutrients to other organisms, and they provide a consistent and high quality source of water within forested basins (Kreye et al. 2014; Panagos et al. 2015; Sun and Vose 2016).
- Generation and maintenance of biodiversity: Forests support most of the terrestrial biological diversity, which benefits humanity through the direct delivery of goods (genetic and biochemical resources) used by humans or through the interaction of complex ecological systems (Daily and Ehrlich 1995).
- Pollination: About one-third of the human diet depends on insect-pollinated vegetables, legumes, and fruits. These pollinators, most of which live only in forested lands, allow for the successful reproduction of innumerable economic and noneconomic flowering plants (Karp et al. 2015; Martins et al. 2015; Quintas-Soriano et al. 2016).
- Natural pest control services: Several species compete with humans for goods and for other provisioning services. One approach to pest control is to use biotechnology or chemical compounds. Another option is to take advantage of biological control species that occur in nature, as many species (e.g., insects such as wasps and other species such as owls and bats) help humans live in forested landscapes (González et al. 2015; Karp et al. 2015; Quintas-Soriano et al. 2016).
- Seed dispersal: Many species of plants need animals as their dispersal agents or require passage through the gut of a bird or mammal before they can germinate. Many of these animals live only in forested lands, and several of the dispersing plant species (e.g., the fruit tree and shrubs species of temperate forests) have a long tradition of bringing goods to humans (Bregman et al. 2015; Karp et al. 2015; Peres et al. 2016).
- Aesthetic beauty, together with intellectual and spiritual stimulation: Human beings have a deep appreciation of natural ecosystems, especially forests, as evidenced by enjoyment of such pursuits as nature photography, bird watching, ecotourism, hiking, and camping. In forests, humans find an unparalleled source of wonderment and inspiration, peace and beauty, fulfillment, and rejuvenation (Daily 1997; Martínez Pastur et al. 2016).

4 Managing for Forest Ecosystem Services

The differences among human-dominated ecosystems, natural ecosystems, and ecosystems built-up through human activity have increased in recent years. Some ES provided by human-dominated ecosystems are traded on formal markets, and society tends to set a higher value on these than is actually due. The other two types of ecosystem are undervalued because their ES are not traded on formal markets, so they do not send price signals that warn of changes in their supply or condition

(Daily et al. 1997). However, the provisioning ES that flow from built-up and natural ecosystems have greatly increased. In response, it is essential to incorporate natural capital and ES into decision-making (Guerry et al. 2015). Costanza et al. (2014) estimated that ecosystems provide at least US$33 trillion dollars' worth of services annually, where about 38% of the estimated value comes from terrestrial systems, mainly from forests (US$4.7 trillion yr.$^{-1}$) and wetlands (US$4.9 trillion. yr.$^{-1}$). Our current economic, political, and social systems are not well suited to the challenge of representing the real value of ecosystems not dominated by human population and activity**.** There is a fundamental asymmetry at the heart of economic systems that rewards short-term production and consumption of marketed commodities, at the expense of stewardship of natural capital necessary for human well-being in the long term. Conservation and economic development have been considered as separate spheres for too long. Sustainable development requires explicit recognition that social and economic development are part of a stable and resilient biosphere (Guerry et al. 2015).

The Millennium Ecosystem Assessment (MEA 2005) combined both the applied and basic motives of sustainability science. It challenged the research community to synthesize what is known about sustainability science in policy-relevant ways, exposing both the strengths and the gaps in the underlying science (Carpenter et al. 2009). As human populations grow, and increasingly disconnect from nature, sustainability requires increasing focus and effort. For this, Guerry et al. (2015) proposed the following strategies to achieve sustainable development: (i) developing solid evidence linking decisions to impacts on natural capital and ES and then to human well-being; (ii) working closely with leaders in governments, businesses, and civil society to develop and make accessible the knowledge, tools, and practices necessary to integrate natural capital and ecosystem services into everyday decision-making; and (iii) reforming policies and institutions and building capacity to better align private short-term goals with societal long-term goals.

Conservation and development come from two distinct agendas: (i) conservationists who seek to increase public support for biodiversity protection by integrating economic development into protection initiatives and (ii) development agencies that seek to provide for the stewardship of nature under the mantra of sustainable development (Tallis et al. 2008). However, to achieve sustainability in ecosystem management, it is not enough to create partial reserves protecting some percentage of nature: the objectives of maintaining ES and biodiversity must be incorporated into intensively managed temperate landscapes at the landscape level (Franklin 1988; Lindenmayer et al. 2012; Gustafsson et al. 2012).

For ecosystem management, which aims to provide sustainable ES to society while also preserving and fostering biodiversity, the divergent disturbance impacts of these goals present a paradox, as they are at the same time risk factors and facilitators of management objectives (Thom and Seidl 2016). Therefore, it is necessary to develop management strategies for forestry which also incorporate broader protection and maintenance of ES and species diversity. It is probable that such new strategies will lead to reduced production of commodities but will increase the provision of ES for the whole of society.

In addition, many of the ES provided by forests are closely associated with ecosystem resilience, the ability of ecosystems to resist stresses and shocks, to absorb disturbance, and to recover from disruptive change (Myers 1996; Levin and Lubchenco 2008). If resilience declines, ES can generally be expected to decline, too. In this framework, proposals for managing forest landscapes which use ES to advance both conservation and human agendas, simultaneously, would benefit from improved scientific understanding of four key issues: sustainable use of ES, trade-offs among different types of ES, the spatial flows of ES, and economic feedbacks in ES markets (Tallis et al. 2008). The role of the market economy in developing this new management process lies in helping to design institutions which will provide incentives for the conservation of important natural systems and will also mediate human impacts on the biosphere so that these natural systems are sustainable (Heal 2000).

MEA (2005) did not, however, deliver a fully operational method for implementing the ES concept, including tools to assist policy-makers and policy-oriented researchers in taking the provisioning of natural goods and services into account (Armsworth et al. 2007). As a result, the ES label is currently used in a range of studies with widely differing aims. This divergence presents a problem for policy-makers as well as researchers because it makes it difficult to assess the credibility of assessment results and reduces the comparability of studies (Seppelt et al. 2011). Yet it is clear that, to strengthen the political relevance of the concept of ES, the scientific basis for its practical implementation must likewise be solidified (Ash et al. 2010).

5 Broader-Scale Consideration of Forest Ecosystem Services and their Sustenance

Even though much has been written on ES in forests, few examples exist in which the concept was effectively included in the planning, conservation, and management of the temperate forest ecosystems around the world. A great many of the studies and land management plans have focused on local scales, especially with respect to the types of ES addressed but also with respect to the land management policies and practices designed to sustain them.

To realize the full potential of the concept, broader-scale analyses of ES are required. We expect that the scale of focus will shift, for both the scientific community and the land managers, toward addressing broader-scale ecosystem services and design plans to sustain them. This paradigm shift to the adoption of a broader-scale consideration of forest ecosystem services will likely be made less daunting by advances in landscape ecological concepts, in remote sensing and GIS technologies and in simulation modeling methodologies.

Adoption of the concept of ES creates will create a significant change in the point of view of scientists, managers, and policy-makers, and studies on land and resource management will inevitably turn to the broader tools of ES types and landscape ecology. Landscape management with multiple objectives is a better solution for most of the urgent problems of our modern society, in which provision services cannot be divorced from either regulation or cultural services. The foundation for this shift is a better understanding of ES on a broad, even global, scale. Such a perspective is required for designing landscapes that serve human well-being while preserving the ecosystems and biodiversity on which that well-being depends.

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Effects of Climate Change on CH_4 and N_2O Fluxes from Temperate and Boreal Forest Soils

Eugenio Díaz-Pinés, Christian Werner, and Klaus Butterbach-Bahl

1 Introduction

Boreal and temperate forests cover 1210 and 680 million ha, respectively (Keenan et al. 2015). In contrast to tropical forests, whose extent is decreasing due to current deforestation activities resulting in huge emissions of greenhouse gases (Roman-Cuesta et al. 2016), the area of boreal forests remained constant, while the area of temperate forests slightly increased in the last 25 years at an average rate of 2.7 million ha a^{-1} (Keenan et al. 2015). In total, boreal and temperate forests cover approximately 13% of the global terrestrial land surface.

Temperate and boreal forests are known to provide a wide range of ecosystem services (e.g., Gamfeldt et al. 2013), including timber production, water regulation, soil protection and erosion control, support of biodiversity, or recreation. The role of forests in regulating the climate has been also well acknowledged, due to their strong potential for sequestering atmospheric CO_2 in its biomass and soils (De Vries et al. 2003; Vesterdal et al. 2008). In contrast to CO_2, the role of forests as both significant sinks and sources of other powerful greenhouse gases, i.e., CH_4 and N_2O has received comparatively little attention. The crucial role played by forests in

E. Díaz-Pinés (✉)
Institute of Soil Research, University of Natural Resources and Life Sciences (BOKU), Vienna, Austria

Institute of Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany
e-mail: eugenio.diaz-pines@boku.ac.at

C. Werner
Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt, Germany

K. Butterbach-Bahl
Institute of Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany

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regulating nutrient cycling is only possible due to the microbial-mediated transformation processes of the soil organic matter, which make nutrients available again for plant metabolism while also resulting in a substantial release of CO_2, as well as CH_4 and N_2O, to the atmosphere.

Temperate and boreal forests represent one of the major global pools of carbon (C) and nitrogen (N), with more than half of the C being stored in soils (Batjes 1996). Pan et al. (2011) estimated that boreal forest ecosystems store approximately 271 ± 22 Pg C, distributed in the living (54 Pg C) and dead biomass (43 Pg C) and in the soils (down to 1 m) (175 Pg C). This estimate excludes some deep organic boreal forest soils, which explains the significant difference with a recent estimate by Bradshaw and Warkentin (2015) (average: 1096 Pg C, range: 367–1715 Pg C), who included peats, or assessments from IPCC (2007) (471 Pg C). However, all estimates agree that 2/3 to ¾ of all C is stored in soils and peats. For temperate forests, Pan et al. (2011) estimated that the living and dead biomass pool is 62 Pg C, approximately equal to the amount of C stored in soils down to 1 m (57 Pg). Global amounts of N in soils down to 1 m are estimated to be 133–140 Pg (Batjes 1996), while only 10 Pg of N is held in the global plant biomass (Davidson 1994). Figure 1 shows the distribution of forests (Fig. 1A), the soil N stocks down to 1 m (Fig. 1B), and the C:N ratio of these soils (Fig. 1C) for the temperate and boreal zones of the

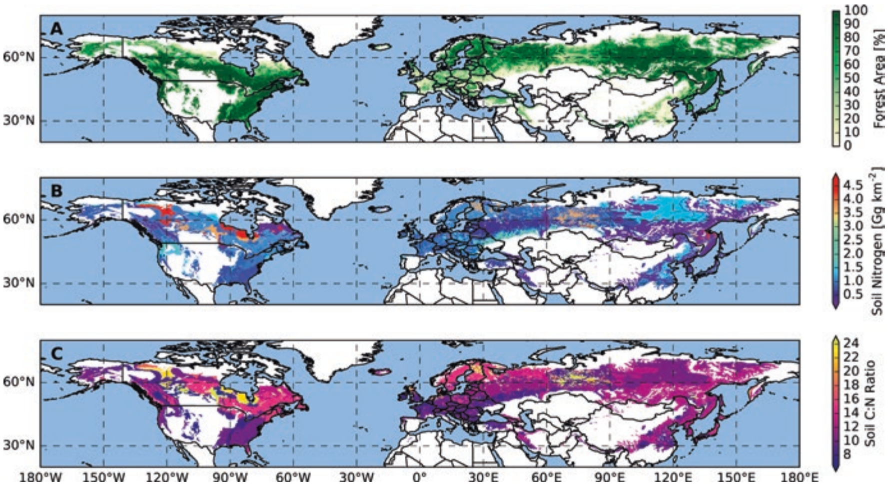

Fig. 1 Distribution of boreal and temperate forests (Panel A), the total nitrogen in soils (Panel B), and C:N ratio of soils (Panel C). The areal extent considered is based on the Olson ecoregions “temperate broadleaf and mixed forests” and “temperate coniferous forest” (Olson et al. 2001). The relative forest cover percentage is based on GlobCover 2009 v2.3 (Bontemps et al. 2011) including the following classes: “mosaic vegetation,” “closed to open broadleaf (B) evergreen (E) forest,” “closed B deciduous (D) forest,” “open BD forest,” “closed needleleaf (N) E forest,” “open NE/ or BE forest,” “closed to open mixed BD/ND forest,” “mosaic forest,” “closed to open B regularly flooded,” “closed B forest permanently flooded.” Spatially explicit soil C and N stocks were derived from the ISRIC-WISE soil map (Batjes 2012)

northern hemisphere. The areal extent considered is based on the Olson ecoregions (Olson et al. 2001), and the relative forest cover percentage (Fig. 1A) is based on the GlobCover 2009 (Bontemps et al. 2011). Spatially explicit soil C and N stocks were derived from the ISRIC-WISE soil map (Batjes 2012). According to this approach, the total soil N stocks in boreal and temperate forest soils are 10.4 Pg N and 7.2 Pg N, respectively.

Globally, both boreal and temperate forest soils have been identified as a source of atmospheric N_2O and as a net sink for atmospheric CH_4. The IPCC 2001 report listed the source strength of temperate forests for atmospheric N_2O with 1.0 Tg N_2O-N a^{-1} (0.1–2.0 Tg N_2O-N a^{-1}), while for boreal forest soils, an estimate was missing. More recently, Dalal and Allen (2008) estimated that boreal forests are a weak source for N_2O (0.33 ± 0.27 Tg N_2O-N a^{-1}) and confirmed earlier estimates for temperate forests (1.05 ± 0.37 Tg N_2O-N a^{-1}). With regard to atmospheric CH_4, Dutaur and Verchot (2007) estimated the sink strength of boreal and temperate forests to be 3.4 ± 5.0 Tg CH_4-C a^{-1} and 2.5 ± 2.6 Tg CH_4-C a^{-1}, respectively. However, since wetland forests were excluded from the study, this estimate is likely biased, because wetlands show net CH_4 emissions at the annual scale. Dalal and Allen (2008) estimated a smaller, more variable sink strength of boreal forest soils (2.0 ± 4.0 Tg CH_4-C a^{-1}), whereas the estimated CH_4 sink strength of temperate forests was with 3.7 ± 0.5 Tg CH_4-C a^{-1} higher and highly constrained.

Climate change refers here to the human-induced alteration of weather patterns, such as temperature and rainfall (amount, frequency, seasonal distribution). Climate change affects soil environmental conditions, as well as landscape hydrology, vegetation cover, and substrate supply. Indirect effects of climate change on land use (e.g., it is expected an agricultural expansion further north (Kicklighter et al. 2014)) are not covered here. Different climate models indicate that the temperate and boreal zones will experience warming in the range of 1.4–5.8 °C by 2100 (Hanewinkel et al. 2013), accompanied by an increase in extreme weather events, which will provoke the shrinkage of permafrost, and the reduction of the snow cover period (IPCC 2013). This will result in changing environmental conditions in both forest canopies and soils, along with shifts of vegetation zones, i.e., upward and northward expansion of the temperate and boreal forest biomes. Alterations of forest species composition, forest growth, and vitality of natural and managed forest landscapes will result in modification of the ecosystem services sustained by forests. While synthesis on the contribution of forests to several ecosystem services is already available (e.g., Millennium Ecosystem Assessment 2005), comprehensive studies linking forests and the exchange of non-CO_2 greenhouse gases between forests and the atmosphere are much more scarce. This chapter aims at evaluating the role of temperate and boreal forests as providers of climate regulation services. Special emphasis is given to the production and consumption of non-CO_2 greenhouse gases by forest soils under changing environmental conditions. Specifically, this chapter assesses how the changes in climate and associated effects may affect temperate and boreal forest soils N_2O and CH_4 fluxes, thereby summarizing existing knowledge and identifying research gaps.

2 Governing Processes and Mechanisms of Forest Soil-Atmosphere CH_4 and N_2O Exchange

Nitrous oxide is mainly produced by the microbial processes of nitrification and denitrification, i.e., an oxidative process converting ammonia/ammonium (NH_3/NH_4^+, classical nitrification) or organic N (heterotrophic nitrification) to nitrate (NO_3^-) and a reductive process, which uses NO_3^- as an electron acceptor for C oxidation to finally convert it to N_2 (denitrification) (Butterbach-Bahl et al. 2013). In these key microbial processes, N_2O is either a facultative (nitrification) or obligate (denitrification) intermediate, which can be released to the soil air, consumed in other parts of the soil profile or finally be emitted to the atmosphere. Although denitrification is considered the most important source of N_2O in forest soils at the European level, nitrification activity also drives total soil N_2O emissions (Ambus et al. 2006). Other microbial processes such as NO_3^- ammonification or physicochemical processes, e.g., chemical decomposition of reactive inorganic N species such as hydroxylamine (NH_2OH) or nitrite (NO_2^-), can lead to N_2O formation too (Butterbach-Bahl et al. 2013). The major controls for N_2O production in forests soils are substrate availability, i.e., NH_3/NH_4^+ and/ or NO_3^- as well as easily degradable C availability (Butterbach-Bahl et al. 2012), temperature (with sensitivity for N_2O emission varying widely) (Brumme 1995; Butterbach-Bahl et al. 1997; Díaz-Pinés et al. 2014; Sitaula and Bakken 1993; Zhang et al. 2016), and soil moisture and soil aeration, as both affect the soil redox potential and thus the preference of reductive processes such as denitrification (Butterbach-Bahl et al. 2013). In addition, soil N_2O emissions are indirectly controlled by tree and associated plant species, forest stand characteristics, and their effects on the abovementioned parameters, soil C:N ratios (Klemedtsson et al. 2005) and soil microbial community composition (Philippot et al. 2009). Finally, the occurrence of extreme events, such as wildfires and pronounced freeze-thaw and soil drying-rewetting cycles (Borken and Matzner 2009; Butterbach-Bahl et al. 2013), strongly affects microbial activity and availability of substrates for N_2O-producing processes.

Methane is predominantly produced in anaerobic, organic-matter-rich microsites of forest soils as a final step of the anaerobic decomposition of organic matter (Conrad 1996). CH_4 production has been observed in both the forest floor and the mineral soil (Butterbach-Bahl and Papen 2002). Forest soils can predominantly function as weak sources of CH_4 (0–20 kg CH_4-C ha^{-1} a^{-1}) if soils are poorly drained or seasonally flooded due to their topographic position in the landscape, such as many aspen or alder stands (Mander et al. 2015; Matson et al. 2009). In upland soils, CH_4 produced at anaerobic microsites or in deeper soil layers is likely to be oxidized while passing through aerobic soil layers. This implies that the observed CH_4 flux at the forest soil-atmosphere interface is the net result of simultaneously occurring production and consumption processes (Conrad 1996). Most of the temperate and boreal forest soils are upland soils, which predominantly function at annual scales as weak sinks for atmospheric CH_4 (0–5 kg CH_4-C ha^{-1} a^{-1}) (Dutaur and Verchot 2007). However, topographically complex ecosystems may lead to spatial fragmentation at the landscape level, with specific locations being net CH_4 sinks while others being strong "hotspot" CH_4 emitters (Nykänen et al. 2003). The CH_4-oxidizing microbial communities are mostly using O_2 – but under certain circumstances also use sulfate or NO_3^- – as electron acceptors (Conrad 2009). High-affinity methanotrophic bacteria found in most forest soils are capable to gain energy from soil atmosphere CH_4 concentrations lower than 1.7 ppmv. Climate change interacts in several ways with CH_4 production and consumption processes in soils. On the one hand, climate change directly affects soil environmental conditions, namely, moisture and temperature, and by this the balance between oxidative and reductive processes, e.g., temperature increases, will – as long as water availability is not limiting – likely result in an increase in aerobic respiration, thus decreasing soil oxygen (O_2) availability and the CH_4 oxidizing capacity of upland soils. On the other hand, global change and increases in atmospheric CO_2 concentration affect plant biomass production and its aboveground-to-belowground ratio, root exudation, and litter quality. All these changes finally modify ecosystem CH_4 exchange, with results being different across different ecosystem types and climatic zones. Finally, climate change also affects regional water balances and thus landscape groundwater levels. This will ultimately control the future distribution of wetlands and emission magnitudes of CH_4 at the landscape scale (Jungkunst and Fiedler 2007).

3 Forest Composition and N_2O and CH_4 Fluxes

Forest tree species composition and tree species richness are of high significance with regard to the provision of economic and ecological services by forests (Gamfeldt et al. 2013). While extensive research has been conducted to elucidate the effect of tree species on biomass production (De Vries et al. 2003), biodiversity (Barbier et al. 2008), water regulation (Ewers et al. 2002), or soil C sequestration (Vesterdal et al. 2008; Díaz-Pinés et al. 2014), our knowledge is rather limited with regard to the relationship between forest composition and its importance for the function of forests as climate regulators, specifically in view of the importance of forest soils as sink or sources of non-CO_2 greenhouse gases.

Individual trees strongly interact with the surrounding environment by, e.g., reducing the amount of light reaching the soil surface, intercepting water in their canopies, taking up water and nutrients from the soil, and returning organic matter back to the soil. Specific tree species usually behave differently (due to, e.g., different growth rates, water or nutritional requirements, or canopy and root system structure) and therefore create distinct ecological conditions and biogeochemical characteristics in both the canopy (radiation levels, microclimate) and the soil (moisture, pH value, or availability of nutrients). Consequently, microbial processes responsible for production and consumption of N_2O and CH_4 in both the forest floor and the mineral soil are usually tree-species-dependent (e.g., Borken et al. 2003; Butterbach-Bahl et al. 2002; Díaz-Pinés et al. 2014).

Litter is an inherent part of nutrient and C cycling in forest ecosystems. Aboveground litter regulates microclimatic conditions by forming a protective layer on the soil surface (Sayer 2006). Litter material from conifers contains high amounts of lignin and tannins, which are mainly decomposed by fungi (Dix and Webster 1995), as opposed to litter originated from deciduous trees (e.g., beech). The latter has simpler chemical structures and can be decomposed by broader spectra of soil microorganisms. This usually provokes that coniferous forests develop a thicker forest floor, which both produces and consumes CH_4 (Butterbach-Bahl and Papen 2002) and probably limits the transport of atmospheric CH_4 into the mineral soil (Borken and Beese 2006; Borken et al. 2003). At the same time, the usually compact and moist litter layer developed under deciduous forest can lead to high N_2O production rates (Pilegaard et al. 2006).

Belowground, rhizodeposition and root decay supply soil microorganisms with C to sustain further microbial decomposition (Cheng and Kuzyakov 2005). This, along with root respiration and water and nutrient uptake, significantly alters important biochemical properties (i.e., soil moisture, pH, O_2 and CO_2 concentrations, and labile C and N concentrations) in the rhizosphere. In a rhizotron experiment, it has been recently found that roots from different tree species affect soil microorganisms and C dynamics in different ways, with *Fraxinus excelsior* showing a higher CH_4 sink and a lower N_2O source strength compared with *Fagus sylvatica* or root-free soil (Fender et al. 2013), underpinning the possible tree-species-dependent root effects on trace gas production in soils.

In addition to the inherent variation of greenhouse gas fluxes along the landscape due to changing environmental conditions, trees can also pose a strong effect on the spatial pattern of N_2O and CH_4 exchange between the soil and the atmosphere (Butterbach-Bahl et al. 2002). It has been observed that fundamental soil properties (e.g., C and N contents, O_2 availability, microbial activity, moisture) strongly vary with distance from the stem (Chang and Matzner 2000) or from the canopy edge (Simón et al. 2013), and this pattern has been found to be tree-species-dependent (Butterbach-Bahl et al. 2002; Van Haren et al. 2010). Further, tree stems can be major conduits for soil-produced CH_4 and N_2O into the atmosphere. The transport may take place through aerenchymous tissues (extra-large intercellular spaces intended to facilitate aeration in the root system) as has been described for alder trees (Rusch and Rennenberg 1998) but also as dissolved gases in the water stream of the xylem. The contribution of tree trunks and tree leaves to the total ecosystem release of N_2O has been estimated to range from 1% to 3% in temperate beech forests (Díaz-Pinés et al. 2015) to 8% in boreal pine forests (Machacova et al. 2016). With regard to CH_4, *Alnus glutinosa* and *Betula pubescens* trees were found to contribute up to 27% of the ecosystem flux of temperate forested wetlands (Pangala et al. 2015). To our knowledge, information on the contribution of trees to the release of N_2O and CH_4 in boreal forested peatlands is not available.

Coniferous forests are predominant in temperate and boreal biomes (Douglas et al. 2014). In the frame of a changing climate, tree species better adapted to warmer temperatures and more tolerant to summer drought are supposed to have an adaptive advantage compared with other more water-sensitive tree species.

Drought-induced decline of Scots pine (*Pinus sylvestris*) stands has been observed already in the Alps (Rebetez and Dobbertin 2004) or in the Pyrenees (Galiano et al. 2010), at the extent of *Quercus* species. In the Rocky Mountains, drought-induced mortality of *Abies* and *Picea* species has also been observed (Bigler et al. 2007). In addition to the vegetation succession in view of changing environmental conditions, forest managers have promoted mixed forests or broadleaf species in the last decades, under the belief of having higher stability against disturbances (Jandl et al. 2007). It has been predicted the areal contribution of coniferous forests will shrink at the extent of broadleaf forests (Hanewinkel et al. 2013), even if we lack a clear understanding of how drought- and heat-induced tree mortality will impact the composition of most forests (Anderegg et al. 2013).

Following the change of forest composition, environmental conditions and soil microbial communities are expected to change, along with the organic matter transformation processes, ultimately leading to different end-, co-, and by-products during microbial N turnover (e.g., N_2O, NO, N_2). There is a substantial number of publications showing higher N_2O emissions in soils under deciduous forests than under coniferous ones (Ambus et al. 2006; Brumme et al. 1999; Butterbach-Bahl et al. 2002; Díaz-Pinés et al. 2014). This has been associated to larger NO losses in conifer forests (Butterbach-Bahl et al. 1997), resulting in higher N_2O:NO ratios (Papen et al. 2003). Recent results from forest floor incubations in European forests support higher NO emissions from coniferous forests but also a N_2O sink potential in the forest floor of deciduous species (Gritsch et al. 2016). Other authors have associated the lower N_2O emissions under conifer forests to a decoupling between N_2O production and reduction processes, resulting in decreased N_2O:N_2 ratios (Menyailo and Hungate 2005). With regard to CH_4, broadleaf forests usually show higher atmospheric CH_4 oxidation rates compared with coniferous ones (Butterbach-Bahl et al. 2002; Maurer et al. 2008), probably due to the distinct CH_4 diffusivity of the forest floor developed under each type of forest (Borken and Beese 2006; Borken et al. 2003). However, direct tree species effects on CH_4 fluxes can interact with soil moisture effects (Menyailo and Hungate 2005).

Tree species composition may change naturally in the course of ecological succession, but human interventions often also actively modulate stand composition and structures. Thus, forest management plays an active role for determining forest composition, which affects the benefits provided by forests in terms of ecosystem services, including its importance as climate regulators. However, the processes responsible for emitting or taking up N_2O or CH_4 are highly dynamic, and they are the result of complex biogeochemical processes and feedbacks and usually show a high temporal and spatial variability (e.g., Brumme et al. 1999; Butterbach-Bahl et al. 2002). Further, the forest composition is strongly influenced by the topography and landscape configuration, which in turn impacts the net exchange of CH_4 and N_2O. Finally, the relevant role of other parameters such as soil texture, precipitation (Borken and Beese 2005), or N limitation (Pilegaard et al. 2006), which may largely overwhelm the direct tree species effects on the net soil-atmosphere N_2O and CH_4 exchange, appeals for more comprehensive studies including not only different tree species but also soil types, N deposition rates, and climatic regions.