1.1 Old-Growth Forest Perception

Most of us, scientists and laymen alike, are deeply fascinated by old-growth forest. We travel to places like the Tongass National Forest¹ in Alaska or the Białowieża National Park² in Poland to enjoy the sight of forests left to their own devices, with their majestic trees, intriguing structure and rare wildlife. For us, the fascination arises from a mixture of interest, aesthetic pleasure and maybe a slight alienation. However, let us hear a different view on old-growth forests:

“There, a desolate tract of land lies, a sad and sullen region, never used as a man’s abode. Its mountains are covered with forests, dark and dense. Trees without bark and without tops, stand bent or half-broken, withered by age. Others, far more than those first ones, lie down full length, only to decay on those heaps of wood already rotten and to suffocate the seedlings that were about to come through. Nature seems to be worn out here; earth – heaped with the ruins of what she brought forth – carries piles of debris, instead of her flowery green, and holds trees loaded with parasitic plants, poisonous fungi and mosses, those impure fruits of rottenness . . .”

The man who wrote these lines in the eighteenth century was the famous French scientist Comte de Buffon, author of the multi-volume book *Histoire Naturelle* (Lepenies 1989). As a naturalist, Buffon was certainly susceptible to the beauties of organismic diversity, and yet he perceived old-growth forests as ugly and hostile. For it to become beautiful, nature had to be tamed and transformed. The French palace gardens with their strictly geometric arrangement of artfully pruned trees perfectly reflect the spirit of Buffon’s time (Gaier 1989). Interestingly, by that time in the eighteenth century, the days where people in Europe had to fear the forests were long over. Wolves and bears had been exterminated, and the bands of robbers had nowhere to hide, since Central Europe was almost devoid of primary forests.

¹http://www.fs.fed.us/r10/tongass/
²http://www.bpn.com.pl/
The engraving in Fig. 1.1 shows the landscape around Jena, Germany, the home of our Max-Planck-Institute for Biogeochemistry, in 1650 (Lepper and Heinrichs 1999). The surrounding hills, which would naturally be covered by a species-rich temperate deciduous forest, had been turned into sheep-runs interspersed with croplands on more level ground. Soils were eroded and wood was a scarce resource. The few places in Europe where remnants of primary forests, and within them parcels of old-growth forests, could be found were either feudal hunting grounds (e.g. Białowieża), or inaccessible land on steep slopes or in swamps. The remaining common forest was over-used as pasture woodland, through collection of firewood and litter raking. European societies responded to this by developing the science of forestry with the primary goal of restoring the wood supply for the boom in industry. Heinrich Cotta (1817), one of the German pioneers of forest science, stated “In former times we had no forest management but plenty of wood, today we have the science but no wood left.” Another important reaction towards the devastation of nature and the industrialisation of human life was the awakening of a positive, almost enthusiastic attitude towards nature in general and forests in particular. This is manifested in countless poems, songs and novels praising the beauty of nature. The European romanticism of the early nineteenth century was probably the first large ecological movement in the Western world (Trepl 1994), but also in the United States, where the deforestation of the Eastern forests was rapidly progressing, novelists like Henry David Thoreau were advocating a simple life in mother nature’s arms. Beyond these extremes of disgust and praise lies the perspective of indigenous communities, who seem to embrace nature as a sacred, living entity and perceive the forests around them with an ‘easy acceptance’ as Steve Comer, a Mahican Indian of North America, nicely expresses it (Standing Woman and Comer 1996).
1.2 Old-Growth Forest Services

Today, a mere 23% of the world’s forest area can be classified as intact (Greenpeace 2006). These intact forests, mostly primary forests located in the tropics and the boreal zone, are the regions where we can still expect to find a large fraction of old-growth forests, i.e. forests that show little signs of past stand-replacing disturbances and that have matured to reach a dynamic equilibrium driven by intrinsic tree population processes. Currently, the area of intact forest in the tropics – and with it the area of old-growth forests – is shrinking at a rate of 0.5% per year. Many developing and threshold countries cut down their forests, as Europeans and North Americans did in the past, to fuel their budding economies, and developed countries like Canada, the United States and Russia also continue to harvest old-growth forests. In the short-term, individual groups and societies might profit from forest destruction. However, with old-growth forest vanishing at an unprecedented pace, mankind as a whole loses the ecosystem services provided by these forests.

What are the ecosystem services provided by old-growth forests? As outlined above, these may be of a spiritual and/or aesthetic nature. However, there are also many profoundly materialistic services such as the provision of genetic resources, non-timber products, and habitat for wildlife (hunting and ecotourism), the sequestration of carbon, the prevention of floods and erosion, to name only a few. Finally, old-growth forests provide cultural services as the object of scientific studies. In Europe we are facing a situation where true lowland old-growth forests are virtually non-existent. Given this reality, we have lost an important reference point for research in forestry and forest ecology. The loss of natural ecosystems is always associated with a loss of information. In retrospective it becomes clear that, in Europe we do not even know what possibly unique services we are lacking today due to the disappearance of old-growth forests, simply because they had vanished long before we could accurately study them.

1.3 Aims and Scope

In the past decades a large number of studies have been conducted in old-growth forests worldwide addressing such diverse topics as carbon, nutrient and water cycling, population dynamics, disturbance regimes, and habitat diversity using a diverse set of approaches and techniques. These include long-term observations,
chronosequences studies, the micro-meteorological eddy covariance technique, stable isotopes, remote-sensing, and modelling, amongst others. This book aims to synthesise current knowledge on the characteristic functioning of old-growth forests to evaluate the consequences of the world-wide loss of this type of ecosystem (Fig. 1.2).

The book is divided into six parts: part I serves as an introduction and lays the definitional foundation for the chapters following. Part II is devoted to aboveground processes, ranging from deadwood dynamics to canopy fluxes. Part III reviews belowground processes and covers the topics of root, nutrient and soil carbon dynamics. Part IV presents regional accounts of tropical and temperate forests in Europe, and North and South America, and the Canadian boreal forest. Part V deals with the human dimension, including the effect of land-use, and technical and political strategies for the protection of old-growth forests.

In the introductory chapters of the book (part I), Wirth et al. (Chap. 2) review definitions of old-growth and critically discuss their usefulness in the context of functional ecology. They also present a meta-analysis that estimates the fractional cover of old-growth forest in different forest biomes without human impact as a reference point. In addition, the plethora of related terms used in the broad context of old-growth forest (pristine, primeval, intact, etc.) is reviewed. Part of the definition of old-growth forest is the presence of old trees. Taking a dendroecological perspective, Schweingruber and Wirth (Chap. 3) explore to what extent trees differ from other life forms (shrubs, herbs) in their longevity. In this context, they also examine the mechanisms underlying the death of cells, tissues and whole plants.

Fig. 1.2 Topics covered by the different chapters in this book. Only the first author is listed. Asterisks Contributions with co-authors
Part II on above-ground processes starts with a contribution by Kutsch et al. (Chap. 4), who follow up on Chap. 3 by asking whether and how tree age and size influence the physiology and productivity of individual trees and forests. This chapter adds new insights to the ongoing debate about ‘age-related decline’ (Ryan et al. 1997). Based on a re-analysis of the dataset of Luyssaert et al. (2007), the authors are able to show that changes in structure exert a stronger control on net primary productivity than age per se. To evaluate the role of changes in species composition on successional trends in productivity, they further analyse two extensive datasets of leaf physiology of temperate and boreal tree species, and are able to identify potential mechanisms that operate against an ‘age-related decline’. Along the same lines, Wirth and Lichstein (Chap. 5) explore how successional species shifts during the old-growth stage control carbon stock changes in the aboveground biomass and in deadwood. They present a novel model that uses widely available tree traits (e.g. maximum height and longevity) to translate qualitative descriptions of successional pathways of 106 forest cover types of North America into quantitative predictions of aboveground carbon stock changes. They compare their results with observed biomass and deadwood trajectories from long-term chronosequences and inventories (see also companion Chap. 14 by Lichstein et al.). Old-growth forests are usually characterised by the presence of very large trees and a complex horizontal and vertical structure. These three elements create a unique understorey environment that differs from earlier successional forests. Based on an extensive review of the literature on old-growth forests in boreal, temperate and tropical biomes, Messier et al. (Chap. 6) review the distinct structural and compositional features that influence the understorey light environment and how such light conditions affect the structure and dynamics of the understorey vegetation. Knohl et al. (Chap. 7) explore the effects of aboveground structural complexity on the ability of old-growth forests to absorb carbon from the atmosphere, their interaction of carbon and water cycle and their sensitivity to climatic variability. To this end the authors review the micro-meteorological literature and the results from paired catchment studies. Woody detritus is an important component of forested ecosystems and particularly of old-growth forests. It can reduce erosion, stores nutrients and water, serves as a seedbed for plants and as a major habitat for decomposers and heterotrophs. Woody detritus also plays an important role in controlling carbon dynamics of forests during succession. Harmon (Chap. 8) reviews the successional dynamics of deadwood and uses a heuristic model to illustrate major controls on carbon trajectories in deadwood.

The opening chapter of Part III on belowground processes is presented by Wardle (Chap. 9) who focusses on the feedbacks between vegetation properties, nutrient leaching and processes driven by the decomposer communities. Based on a review of millennial chronosequences across the world, he depicts the inevitable fate of all old-growth forests under the absence of disturbance: a progressive ecosystem retrogression driven by phosphorous losses that induces a decline in species diversity and productivity over long time-scales. The function and distribution of roots and their association with mycorrhizal fungi plays a pivotal role in forest ecosystems for soil carbon storage and nutrient and water retention. Bauhus
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