

Chapter 2

Old-Growth Forest Definitions: a Pragmatic View

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2.1 Introduction

Many of us possess an archetype of old-growth forest appearance. We expect majestic trees, small pockets of regenerating trees thriving to reach the sun, heaps of dead wood covered with mosses, snags spangled with cavities and bracket fungi, and rare wildlife. However, thinking twice we may realise that this archetype (1) is not a scientific definition but merely a picture, and (2) is not generic but rather describes the late stage of succession in the temperate forest biome where the great majority of ecologists live and work. In boreal forests, trees rarely reach majestic dimensions and yet may attain great ages. In some pine forests trees become very old, but gap phase regeneration is impeded by recurring surface fires. In tropical forests trees grow tall, but dead wood does not pile up because of high decomposition rates. These examples illustrate that there are many ways for a forest to grow old, and that it is probably a futile task to aim at providing a concise scientific definition of old-growth forest that encompasses the full spectrum of successional and structural options.

This chapter consists of four sections. Section 2.2 reviews existing attempts to define old-growth forest and discusses their merits and problems. Subsequent sections are devoted to the more applied aspects of old-growth forest definitions and their implications. Specifically, Sect. 2.3 presents a literature analysis conducted to understand how the term ‘old-growth’ is actually used in the literature, as well as how often and why it is replaced by competing terms. Section 2.4 explores how disturbance regimes and successional dynamics interact in determining the occurrence of old-growth across the globe, and the topic of old-growth forest conservation is briefly covered in Sect. 2.5. The chapter concludes by discussing the usefulness of definitions in the context of the functional focus of this book.

2.2 Old-Growth Forest Definitions and their Limitations

Simple definitions based on a single criterion are rare in ecology, especially if the *definiendum* ('old-growth forest') is itself a complex dynamic system that is a result of gradual transitions involving several processes. Most definitions today employ multiple criteria (Spies et al. 1988; Hunter 1989; Wells et al. 1998; Messier and Kneeshaw 1999; Kimmins 2003) and these criteria broadly fall into three groups: The first group emphasises structural and compositional features; the second highlights the successional processes that have led to, and currently maintain, the old-growth stage; while the third group summarises criteria related to biogeochemical processes. Figure 2.1 lists a number of criteria and shows how often they have been used in 39 different publications devoted to defining the term 'old-growth' (adapted from Kneeshaw and Burton 1998). It is immediately apparent that existing definitions are based largely on structural criteria, with successional and biogeochemical criteria being less often employed. In the following, the most important structural, successional and biogeochemical criteria will be introduced and critically discussed.

2.2.1 Structural Definitions

2.2.1.1 Criteria

Structural old-growth criteria are based on data relating to age distributions, size distributions and spatial patterns of both live and dead trees, and they are basically formulated to identify stands with gap phase dynamics (Wells et al. 1998). Among these indicators, the data on age structure are the most valuable because they are directly linked with the birth and death events causing these dynamics. The following three criteria for age structure proposed by Mosseler et al. (2003) summarise the most important aspects: (1) uneven, multi-modal or inverse J-shaped age structure; (2) mean age of dominant species approaches half the maximum longevity for the respective species; and (3) some old trees are close to their maximum longevity. Diameter or height distributions are often used as a proxy for age distributions assuming that age and size are reasonably well correlated (but see below). An inverse J-shaped size distribution usually translates into a complex, multi-layered canopy structure (Franklin and Van Pelt 2004). Mortality of canopy trees is a prerequisite for gap phase regeneration. Large standing dead trees and coarse woody detritus on the forest floor are indirect evidence of this process, and their presence is often used as another structural indicator of gap phase dynamics (Harmon et al. 1986). A typical criterion is therefore the presence of large amounts of standing and downed dead wood in all stages of decay. Another indicative structural feature of old-growth forests is the pit-and-mound micro-topography that forms at the forest floor if large trees are uprooted (Lorimer and Frelich

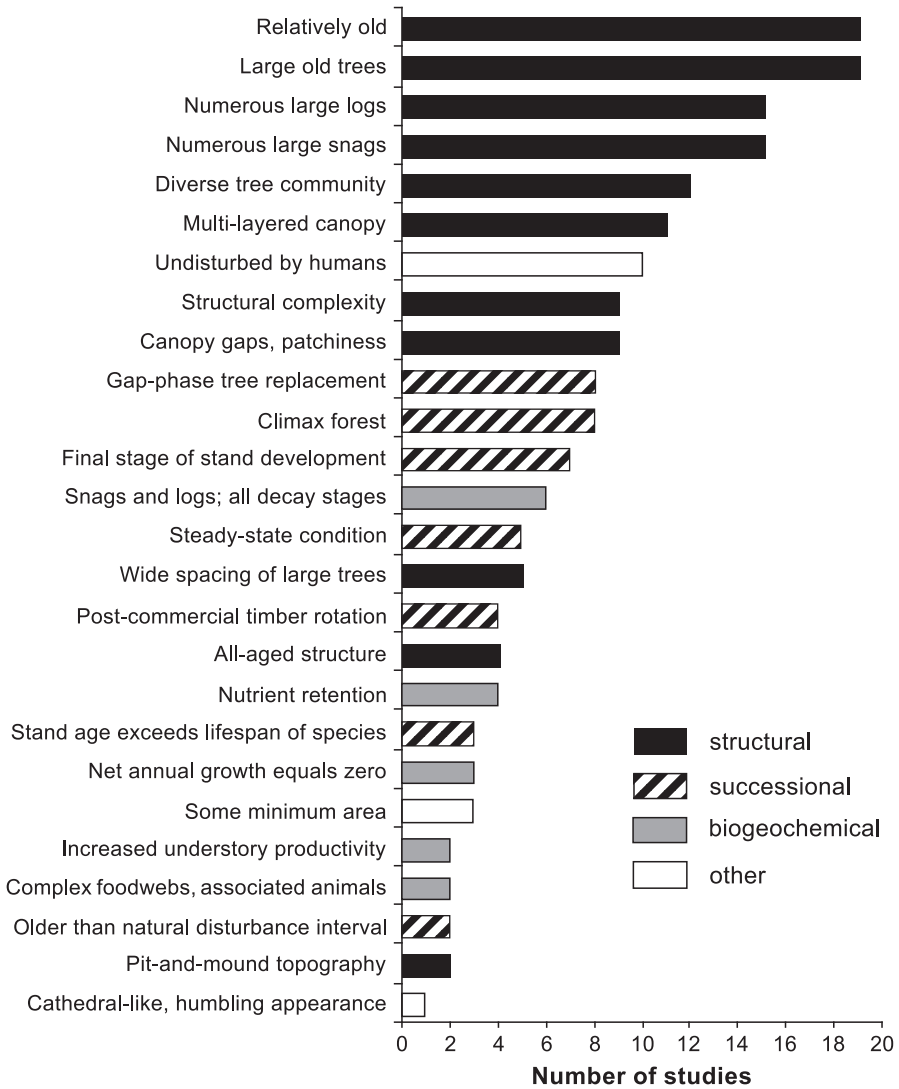


Fig. 2.1 Chart showing how often different criteria have been mentioned in a total of 39 publications devoted to the subject of defining old-growth forest (adopted from Table 1 in Kneeshaw and Burton 1998). The three main categories of old-growth criteria (“structural”, “successional” and “biogeochemical”) are indicated by the black and patterned bars; terms that fall into none of these three categories are shown as “other” (white bars)

1994; Liechty et al. 1997), but similar conditions can exist in young stands regenerating after major wind blow. Interestingly, spatial pattern analysis is rarely used as a means of quantifying the degree of ‘gapiness’ although stand maps are often available (but see, e.g. Getzin et al. 2006; Harper et al. 2006).

2.2.1.2 Limitations

The major limitation of structural indicators is that they have been developed to characterise old-growth appearance in a very limited set of forest types (Spies 2004). Many of the pivotal papers on old-growth definitions (Spies et al. 1988; Franklin and Spies 1991; Wells et al. 1998; Messier and Kneeshaw 1999; Kimmins 2003) have been written by scientists who worked in the Douglas-fir/Western hemlock forests of the Pacific North-West of the United States or British Columbia. The derived structural indicators are not easily transferred to other forest types – not even in qualitative terms. Bergeron et al. (Chap. 13, this volume) demonstrate the limited validity of typical old-growth indicators using a number of boreal forest types as examples.

As a more practical concern, the determination of tree ages for the establishment of age distributions is not without problems. First of all, it is very time-consuming. For example, in a pivotal study analysing 13 stands for old-growth characteristics, Kneeshaw and Burton (1998) determined the age of a total of 2,720 trees. Not only does this represent a substantial effort, but it is also prone to substantial error if not done correctly. This is especially true in old-growth forests where advance regeneration may be suppressed for up to a century, i.e. the pith of a core taken at breast height may have been the terminal shoot of a 100-year-old tree (Oliver and Larson 1996, pp 137–140). Even coring at base height does not solve the problem entirely because the oldest pith dates are often found well below the root collar. This is because many trees were bent down as saplings by snow or fallen logs, and have developed adventitious roots (Parent et al. 2002). Under these conditions, correct ageing requires sophisticated techniques such as cross-dating or pith node counting (Nilsson et al. 2002). If trees have regenerated through resprouting, only the ramet age can be determined but not the age of the individual tree (see Chap. 3 by Schweingruber, this volume). In the tropics, most tree species do not form annual rings and only a few species deposit annual parenchyma bands, which are difficult to identify under field conditions (Worbes 1999). Therefore, age determination often rests upon indirect methods based on size-growth rate relationships (Lieberman et al. 1985) or very expensive methods using radiocarbon dating (Horvitz and Sternberg 1999; Fichtler et al. 2003). Because of these problems, diameter distribution data are usually employed as a proxy for age distribution. However, this approach suffers from similar problems, because in datasets including suppressed saplings age and size are often poorly correlated, tending to follow a triangular relationship (Schulze et al. 2005).

Using the amount and size of deadwood as sole indicator may potentially be misleading (see also Chap. 8 by Harmon, this volume). First, dead wood stocks often exhibit a U-shaped pattern over succession (Harmon et al. 1986; Kimmins 2003). Since most stand-initiating disturbances (including fire) do not remove coarse woody material, early stages of succession are often characterised by high loads of large-sized legacy dead wood – both standing and downed – of all decay classes. The structural characterisation of dead wood in terms of size, abundance

and decay state is therefore not a good indicator of old-growth conditions unless accompanied by additional information on stand structure and history. For example, if age distribution data suggest a long period without stand-replacing disturbances, the presence of strongly decayed large-sized coarse woody detritus ensures that single tree mortality and gap opening has been a stand feature for an extended period of time.

Second, because of elevated decay rates in warm and humid climates, deadwood stocks in tropical forests are generally low. Using the coarse woody debris database compiled by Mark and Janice Harmon¹, we calculated that median coarse woody detritus (CWD) decomposition rates, k , in tropical regions below 25° latitude are 0.221 year⁻¹ (10%–90% percentile: 0.053–0.607 year⁻¹, $n = 32$), i.e. a factor six higher than decay rates in the extra-tropics [0.038 year⁻¹ (0.009–0.127 year⁻¹); $n = 179$]. These decay rates translate into deadwood lifetimes (time after which 95% of the original material has decayed) of 14 years in the tropics versus 80 years outside the tropics. With a given input of deadwood I and decay constant k , the equilibrium stocks of CWD can be simply calculated as I/k (Olson 1963). It follows that, even if we assume double input in the tropics, CWD stocks in the tropics are still lower by a factor of three than in temperate and boreal zones.

Finally, static structural definitions fail where changes in structural attributes are a characteristic feature of a particular forest ecosystem. Forests subject to recurring surface fires exhibit very different spatial patterns and size and age distributions depending on the timing of the last fire event (Sannikov and Goldammer 1996; Wirth et al. 1999; Spies 2004; Spies et al. 2006).

2.2.2 Successional Definitions

2.2.2.1 Criteria

An important criterion grounded in succession theory was given by Oliver and Larson (1996), according to which the term *true* old-growth “*describes stands composed entirely of trees which have developed in the absence of allogenic processes*”. In its original meaning, the term *allogenic* refers to all external processes freeing available growing space, as opposed to *autogenic processes*, where changes in available growing space are caused by plant interactions (Tansley 1935). In the above definition – although not explicitly stated – *allogenic processes* refers to large-scale disturbances like fire, harvest or major wind-throw, which have the potential to reset secondary succession, but excludes external continuous forcing such as changes in climate. Secondary succession usually starts with pioneer species that possess a suit of traits enabling them to colonise and thrive on disturbed ground – high output of far-travelling seeds, seedlings with high desiccation and high-light

¹http://afoludata.jrc.it/carboinvent/cidb_cwdgdb.cfm

tolerance, high nutrient acquisition rates and growth rates, to name only a few (Horn 1974). Fast growth rates are often realised at the expense of chemical defence and/or mechanical stability, with the consequence that pioneers are mostly short-lived (Loehle 1998). One way to interpret the above criterion is to define true old-growth as the phase after which this first cohort of pioneers has disappeared and the stand is taken over by mid- and late-successional species that arrived later (true old-growth in Fig. 2.2a). Using the average life-time of temperate and boreal pioneer species given in Wirth and Lichstein (Chap. 5, this volume; see also Fig. 2.7), this is the case after about 100–150 years in the respective biomes. In the tropics, pioneers turn over even faster and the old-growth phase may be reached already after 80 years (Lieberman et al. 1985; Laurance et al. 2004). However, one could argue that mid-successional species are also “delayed pioneers” that profit indirectly from conditions created by allogenic processes, and that may not be able to persist under true old-growth conditions. With this interpretation, the true old-growth stage would commence much later. In any case, the successional concept of Oliver and Larson, (1996) clearly focusses on processes leading to old-growth, namely the replacement of early- (or mid-) by late-successional species. This concept ignores structural aspects and does not contain any statements about the absolute size and age of stands. To apply successional criterion data on forest composition and establishment, history of trees is required. Other successional definitions highlight processes that maintain old-growth, such as the type of prevailing disturbances (presence of small-scale and absence of stand-replacing disturbances), gap phase or nurse-log regeneration, or high shade tolerance of dominant species (Mosseler et al. 2003).

2.2.2.2 Limitations

Oliver and Larson’s (1996) successional criterion for old-growth requires that the initial post-disturbance cohort of trees is replaced by tree species capable of gap phase regeneration. This definition is problematic in forest successions containing long-lived pioneer species. These share several features of typical pioneers (colonising ability, high light requirements and tolerance) but may well live for 300 years and more (Peet 1992; Lusk 1999; Spies 2004). Hence, they may still be present in old stands that meet most structural criteria for old-growth. They are often found in forest communities of xeric habitats (e.g. species of the genera *Pinus*, *Quercus*, *Juniperus*) but may also occur on mesic sites (e.g. species of the genera *Picea*, *Fraxinus*, *Liquidambar*, *Pseudotsuga*, *Nothofagus*). In boreal and high-elevation forests, late-successional species of the genera *Abies* and *Picea* often invade disturbed areas simultaneously with broad-leaved pioneers of the genera *Betula* and *Populus* (Schulze et al. 2005). Such late-successional species act as long-lived pioneers that undergo an initial phase of suppression and will eventually replace themselves. Under all these circumstances, stands would enter the true old-growth stage *sensu* Oliver and Larson (1996) only very late (>300 years) after the long-lived pioneers have also been replaced (true old-growth in Fig. 2.2b). An extreme case is presented by very old (~400 years), even-aged Scots pine stands

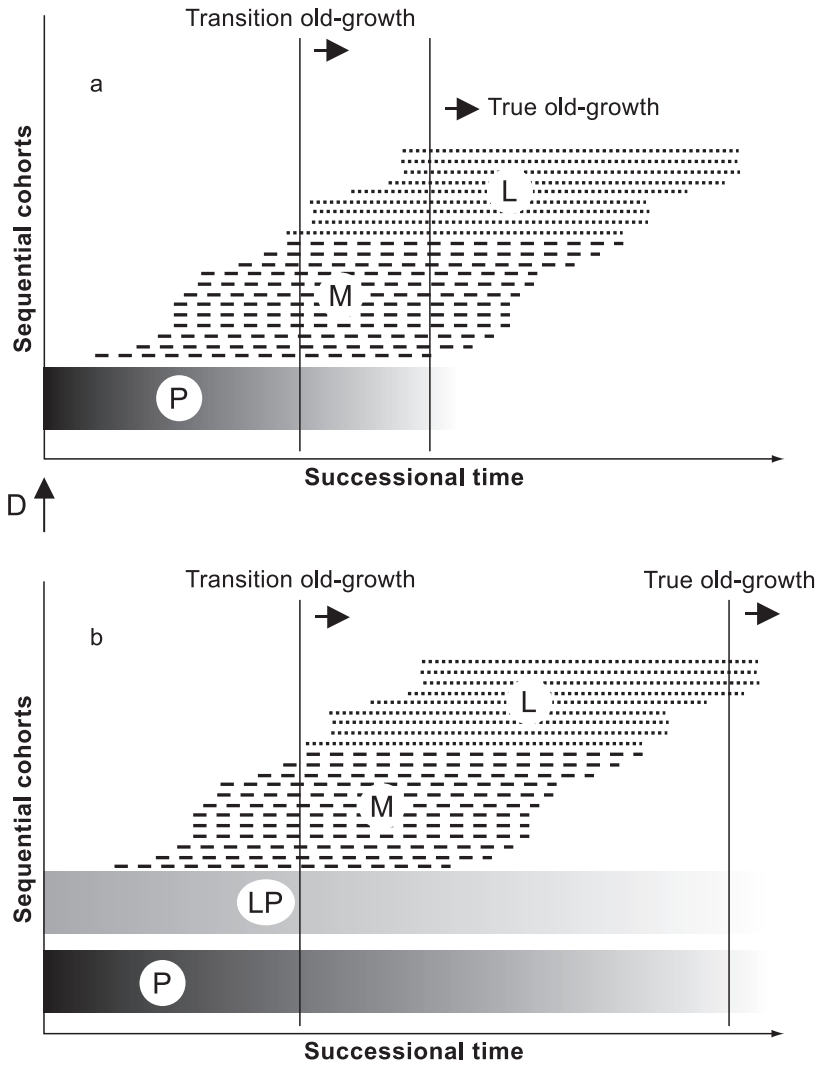


Fig. 2.2 a,b Conceptual illustration of successional criteria of old-growth. According to Oliver and Larson (1996), the true old-growth stage is reached when all individuals have regenerated in the absence of allogenic processes initiating stand development. **a** Immediately after a stand-replacing disturbance the site is colonised by pioneers (*P*). After some time the first individuals of mid-successional species (*M*) become established, followed by late successional species (*L*) later on. True old-growth conditions are reached when the regeneration wave of pioneers has disappeared. For transition old-growth, a minor component of pioneers is acceptable but late-successional are already an important component of the stand. **b** True old-growth conditions are reached much later if long-lived pioneers (*LP*) are present in the mixture. The onset of the transition old-growth stage is not affected

(a typical pioneer species) on sandy soils in boreal Eurasia where surface fires keep out fire-sensitive late-successional species (Wirth et al. 1999). As a ‘soft’ version of the successional definition, Oliver and Larson (1996) introduced the term *transitional* old-growth (Fig. 2.2a,b), which characterises the phase where a reduced number of pioneer individuals may coexist with mid- and late-successional species in advanced stages of succession. The application of this term mitigates some of the problems mentioned above, however at the expense of definitional clarity, because the start of the phase of transitional old-growth is difficult to determine.

2.2.3 Biogeochemical Definitions

2.2.3.1 Criteria

Biogeochemical criteria are undoubtedly the most difficult to apply and therefore also the least reported. Examples of biogeochemical criteria that have been listed as indicative of old-growth conditions are closed nutrient cycles, reduced tree net primary production (NPP), zero net accumulation of biomass, and increased understorey vegetation.

2.2.3.2 Limitations

Even if one were to agree that a decline in NPP, a biomass equilibrium and closed nutrient cycles are in fact indicative of old-growth conditions (but see Chap. 21 by Wirth, this volume), the quantification of almost all of these parameters is extremely labour-intensive and requires expensive instrumentation and extended observation periods (Sala et al. 2000). For example, the quantification of net primary productivity involves, as a minimum requirement, the measurement of tree ring widths and wood density of stems, branches and coarse roots, the estimation of foliage and fine-root biomass and turnover, a full stand inventory, and the development of suitable allometric equations for scaling up of sample tree information (Lauenroth 2000; Sala and Austin 2000; Clark et al. 2001). In short, biogeochemical criteria represent typical results of multi-year ecosystem studies and thus certainly do not qualify as easy measures for identifying old-growth forests.

Besides such practical considerations, there is a more philosophical objection against including functional attributes as part of a definition. In science, a definition is useful when it allows the scientist to unambiguously identify an object that, in a second step, may become subject to a more detailed characterisation. In the context of this book, biogeochemical functions represent ‘response variables’ (see below) and should not be confused with criteria defining the term ‘old-growth’.

2.3 Use of the Term “Old-Growth” – a Literature Survey

According to the philosopher Karl Popper (1994) it is not the definition that dictates the application of a term, but rather the application of a term that shapes its definition. Thus, as an alternative to conducting a scholarly analysis of existing definitions as done above, it is also instructive to analyse how scientists and land-managers actually use the term *old-growth* and – most importantly – whether they use the term at all. Definitional problems are usually aggravated by the fact that there are related terms that are commonly used and confused. Scoping the ecological literature, we find a plethora of competing terms in the most diverse contexts: ancient, antique, climax, frontier, heritage, indigenous, intact, late-seral, late-successional, natural, original, over-mature, pre-settlement, primary, primeval, pristine, relict, untouched, virgin. This list is not exhaustive and there is neither the space nor the necessity to discuss each of these terms individually. Ignoring subtle differences they fall broadly into two groups (Fig. 2.3). The first group specifies forests or forest

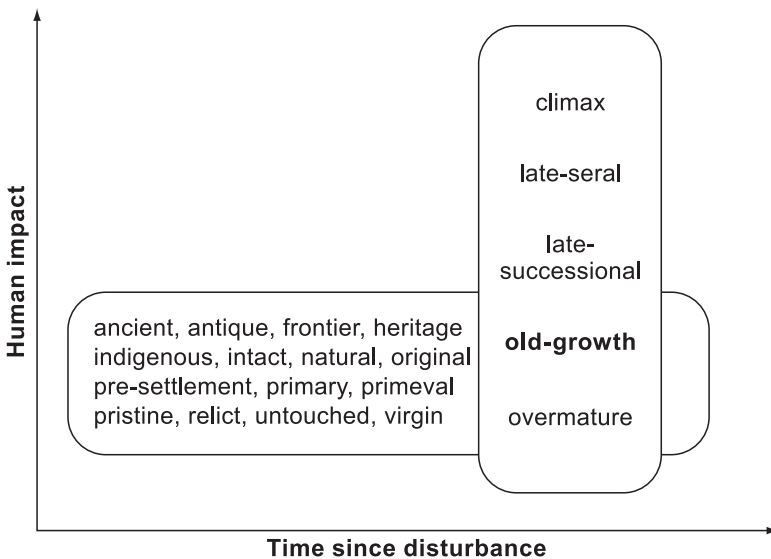


Fig. 2.3 The most important terms used in the context of forest conservation that may be used erroneously in place of ‘old-growth’. The terms are arranged in a semantic space defined by two axes: degree of human impact (y-axis) and time since the last stand-replacing disturbance (x-axis). The majority of terms (*horizontal box*) describe stands that have been subject to very low levels of human impact for an extended period of time. This includes stands of any age and time since disturbance. On the other hand, the terms in the vertical box denote stands that have reached a certain age or late successional stage and that may or may not have been impacted by humans. For example, old-growth stands may originate from a planted stand developing after clear-cut. In this book we use the term ‘primary’ to characterise the former, and the term ‘old-growth’ to refer to the latter category

landscapes that have never or only rarely been impacted by humans. The second group is closer to the definition of old-growth and emphasises the fact that forests are relatively old. Whenever we want to refer to the former category we will use the term 'primary' in this book. We surveyed the Web of Science database to address the following questions: How often is the term old-growth used in relation to potentially competing terms? Has the terminology changed over time? Does the terminology differ between ecological sub-disciplines and scientific communities? Finally, how old are forests that were labelled 'old-growth' really?

Covering three time periods (1940–1960, 1970–1980 and 1995–2005), we searched for papers containing the keyword 'old-growth' (or 'old growth') and the seven most common competing terms: 'natural', 'pre-settlement', 'primary', 'primeval', 'pristine', 'relict', 'virgin'. Next, we screened all abstracts and selected only those studies that addressed the topics conservation, general ecology, and ecosystem science. This resulted in a total of 2,153 papers for the three periods. For each paper we recorded the home country of the main author based on the author's address. It should be noted that this is not necessarily the country where the study sites were located, but rather specifies which regional scientific community the main author belongs to. Where given in the abstract, forest ages associated with old-growth stands were recorded. Hereby, we distinguished between estimated stand ages and age thresholds. If a range of stand ages was given we calculated the central value as $(\min + \max)/2$. This analysis ignores studies that are not listed in the Web of Science and those published in languages other than English (e.g. the majority of European publications on forestry prior to 1950 were published in German, French, or Russian).

If we first look at the development of the total number of publications over time we observe a slight increase in the number of publications from 9 per decade between 1940 and 1960, to 46 per decade between 1970 and 1980, followed by a sudden jump to 2,089 per decade between 1995 and 2005 (Fig. 2.4a, top panel). This does not necessarily mirror the real trend in paper output as the Web of Science coverage of publications is certainly higher today than in the 1950s. However, the recent explosion in paper output is certainly not consistent with the general law of information science, according to which the body of literature in the natural sciences doubles every 10 years. We may thus speculate that this current boom can also be ascribed to a renewed interest in, and an increasing awareness of the threat to, old-growth forests.

In the 18 early studies published before 1960, the term old-growth was used only once in a paper on molluscs (Jacot 1935). The most common term in those days was 'virgin' forest ($n = 13$; Fig. 2.4a). Although in its original meaning 'virgin' merely means untouched by humans, most studied forests clearly qualify as old-growth in a contemporary sense (Morey 1936; Meyer and Stevenson 1943; Oosting and Billings 1951; Oosting and Reed 1952; Grier et al. 1992). In the 1970s the percentage of studies referring to old-growth increased to 39%, closely followed by 'natural' forests (37%); 13% used the term 'primeval' and only 9% referred to 'virgin' forests. Today (1995–2005) 'old-growth' has become the most widely used term, occurring in 62% of all publications; 13% still use the term 'natural' and all other

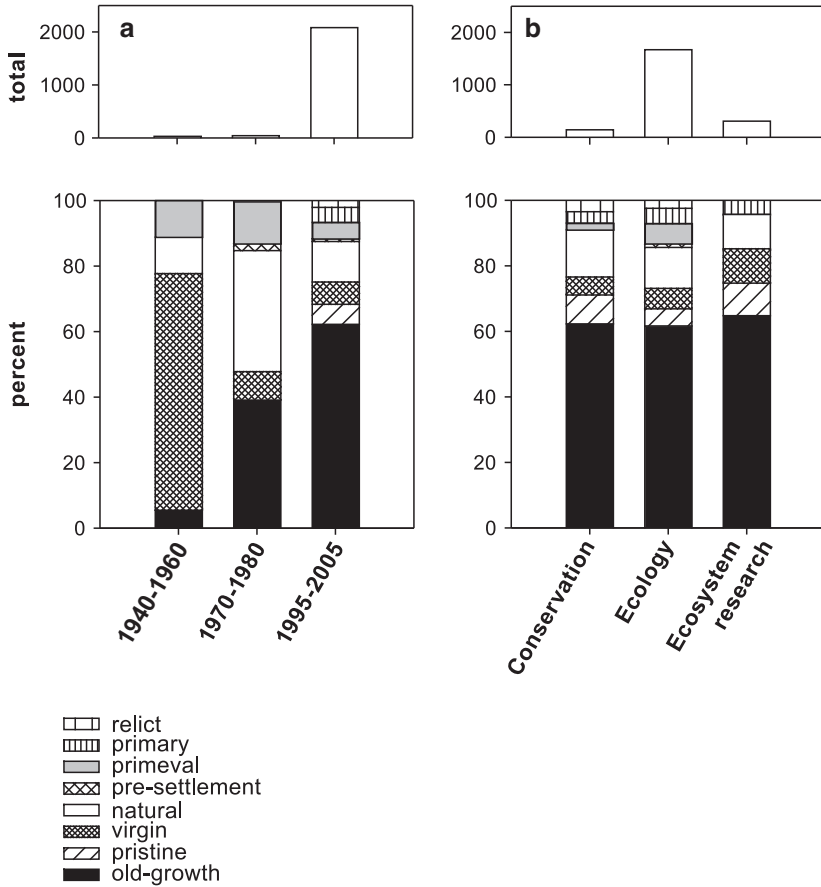


Fig. 2.4 Literature analysis based on 2,153 publication from three periods (1940–1960, 1970–1980 and 1995–2005). **a** Temporal development of the usage of the term ‘old-growth’ in relation to seven competing terms: ‘natural’, ‘pre-settlement’, ‘primary’, ‘primeval’, ‘pristine’, ‘relict’, ‘virgin’ (lower panel, see key). **b** Comparison of the three ecological sub-disciplines conservation, ecology and ecosystem research with respect to usage of the term ‘old-growth’ in relation to the seven competing terms. The top panels show the absolute numbers of publications

terms are used only occasionally. The increase in importance is probably due to the fact that many of the pivotal papers on the definition of old-growth were written only recently (Wells et al. 1998; Kneeshaw and Burton 1998; Mosseler et al. 2003; Gratzner et al. 2004).

While there were only subtle differences in the use of terms between the three disciplines conservation biology, general ecology and ecosystem science (Fig. 2.4b), the terminology spectrum depended strongly on the first author’s nationality (Fig. 2.5). The great majority of North American publications (80%) used the term ‘old-growth’. The same is true for Scandinavian countries (N-Europe), Australia and New Zealand, Chile, Argentina, and Japan – all countries with

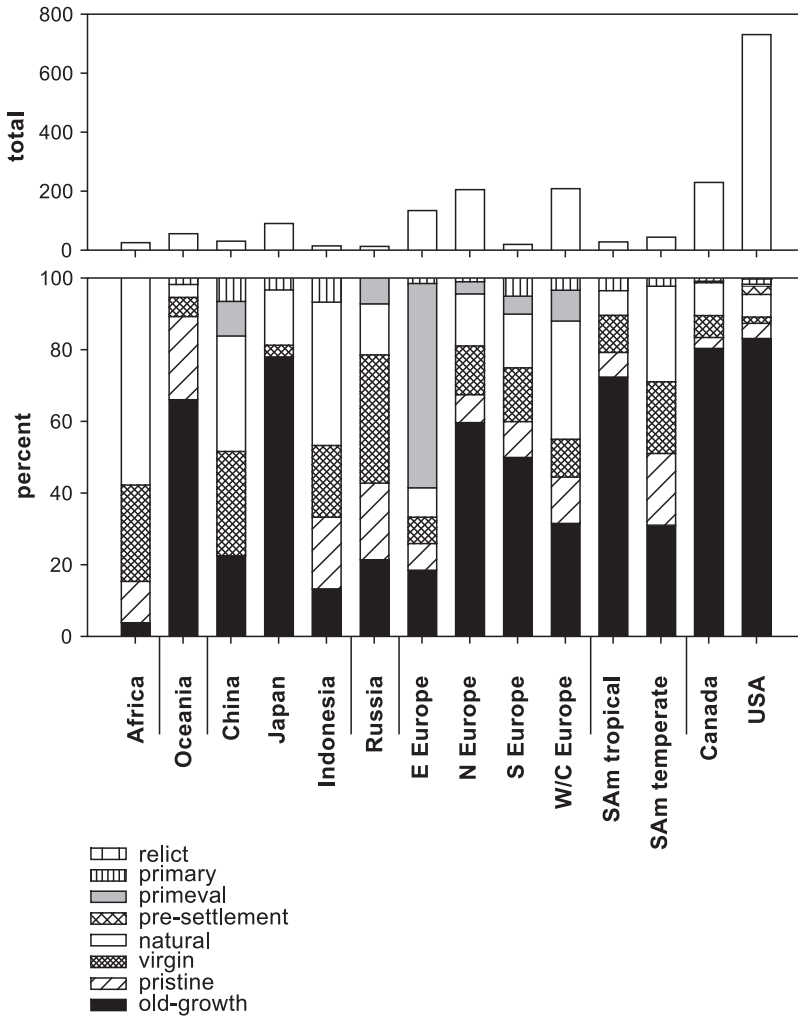


Fig. 2.5 Regional comparison of the usage of the term ‘old-growth’ in relation to the seven competing terms ‘natural’, ‘pre-settlement’, ‘primary’, ‘primeval’, ‘pristine’, ‘relict’, and ‘virgin’. Regions were assigned based on the address of the first author, which may differ from the actual location of the study site. *E* Eastern, *N* northern, *S* southern, *W/C* western/central, *SAM* South America

close relationships to the United States scientific community. Taking Chile as an example, we find that out of the 17 relevant publications 13 were co-authored by United States scientists and the remaining 4 included Juan J. Armesto, who received his PhD in the United States, as a co-author. Authors from Central and Western European countries rarely used the term ‘old-growth’, most likely because forests meeting the criteria for old-growth barely exist here and can only be studied abroad (see Chap. 15 by Schulze et al., this volume). However, this is not true for the

Eastern European countries and Russia, which do possess remnants of ‘old-growth’ forest and yet do not use this term. Instead the term ‘primeval’ is preferred; this is clearly due to the fact that the famous Biatowieża National Park in Poland carries the attribute ‘primeval’ in its name (Biatowieża Primeval Forest). Of 135 Eastern European investigations, 91 were conducted in Biatowieża. Another region where the term ‘old-growth’ is rarely used is the tropics (Africa, tropical Latin America, and Indonesia). First of all, only a few studies ($n = 86$) exist where the first author resides in a tropical country. Of these 86 studies, only 17 used ‘old-growth’, while 33 used the term ‘natural’. We speculate that this is because old-growth conditions are nothing special in the tropics and thus need not be emphasised (see Fig. 2.7).

Finally, we wanted to know the stand age of forests that were labelled as ‘old-growth’. Altogether we identified 118 studies where ages of old-growth forests were reported, half of which were temperate or high-elevation coniferous forests and 25 were communities dominated by Douglas fir (*Pseudotsuga menziesii*), one of the classical ‘majestic’ old-growth species in the north-western United States. Old-growth forest ages ranged from 50 to 1,150 years (Fig. 2.6). The youngest ‘old-growth’ stand was a mangrove stand (Bird et al. 2004), and the oldest a montane

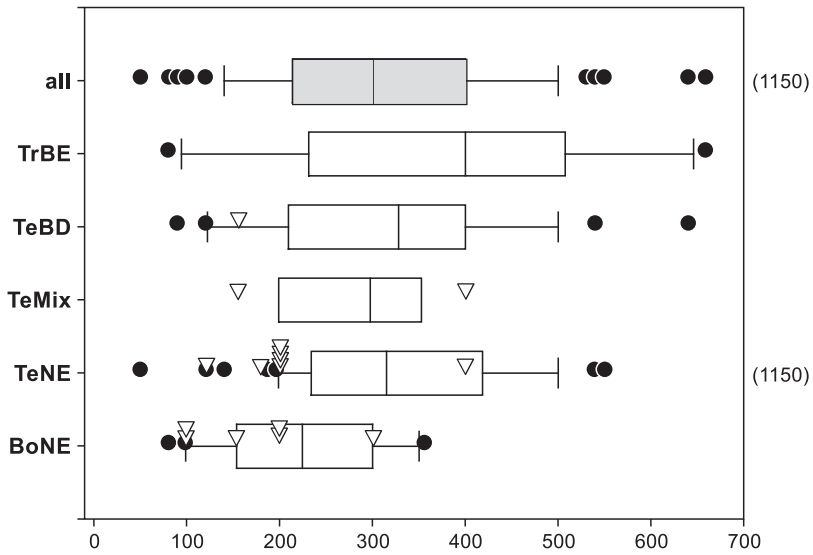


Fig. 2.6 Age range for forest stands reported to be in the old-growth stage separated according to forest type: *BoNE* boreal needle-leaved evergreen ($n = 14$), *TeNE* temperate needle-leaved evergreen ($n = 41$, this group contains also temperate rainforest and high-elevation conifer stands), *TeMix* temperate mixed forest ($n = 4$), *TeBD* temperate broad-leaved deciduous ($n = 14$), *TrBE* tropical broad-leaved evergreen ($n = 7$). Boxes interquartile range; error bars 10%- and 90%-percentile range for forest types with $n > 6$; filled circles outliers; open triangles papers making reference to age thresholds, e.g. claiming that any stand older than x years was considered old-growth; values in brackets extreme values

fir-hemlock forest on the coast of British Columbia (Parish and Antos 2004). The median age of all forests was 300 years with an inter-quartile range of 210–400 years. This corresponded to the old-growth ages of the three temperate forest types with median ages close to 300 years (temperate needle-leaved: 315 years; temperate mixed: 289 years; temperate deciduous: 313 years). Boreal old-growth forests were somewhat younger (median age 224 years, inter-quartile range 150–300 years), whereas tropical old-growth forests tended to be older (median age 400 years, inter-quartile range 230–508 years). This is surprising as the analysis above suggested that tropical forests reach the old-growth stage much earlier, and they are also more common than boreal forests. To further examine why several studies ($n = 19$) identified stands younger than 200 years as old-growth we had a closer look at the species composition. Against our expectations, most stands were dominated by long-lived species. Extreme cases of suspiciously young ‘old-growth’ forests are 60- to 120-year-old oak stands (Laiolo et al. 2003), a 100-year-old boreal Norway spruce stand (Dahlberg et al. 1997), and a 110-year-old Balsam fir stand (Sturtevant et al. 1997). There seemed to be reasonable agreement between reported age thresholds and actual stand ages. The overall median threshold across forest types was 200 years, which corresponded quite well with the lower quartile range of 210 years. This is in agreement with the minimum age criteria developed for the western United States, which ranges between 150 and 200 years (Wells et al. 1998).

2.4 Old-Growth and the Disturbance Spectrum

The relationship between the disturbance regime and the occurrence of old-growth forest is so fundamental that it deserves a separate discussion. Depending on their severity, disturbances may promote or destroy old-growth. In the following, we will discuss the importance of both the temporal and spatial scale of disturbances on old-growth forest occurrence in the world’s largest forest biomes.

2.4.1 *Temporal Scale*

In most forest types, irrespective of the definition applied, it may take several centuries before old-growth conditions develop. At the same time, forest landscapes are subject to stand-replacing disturbances such as wildfires, wind-throw, insect infestations or harvest, which terminate the old-growth stage or development towards it. Obviously, the potential of a forest region to host old-growth forests depends on two rates: (1) the time it takes for old-growth to develop, and (2) how often succession is set back by disturbances. In the following we will develop a simple theoretical framework to quantify this potential for different forest types based on data on species longevities and disturbance regimes obtained from the literature. Adopting the successional definition despite its limitations, we define the

time to reach true old-growth conditions, t_{og} , as the time it takes for the initial cohort to disappear. As an estimate of t_{og} we use the maximum longevity of typical pioneer tree species (Lieberman et al. 1985; Ellenberg 1986; Burns and Honkala 1990; Nikolov and Helmisaari 1992; Laurance et al. 2004). Imagine that we know the distribution of stand ages on the landscape. In this case the fraction of old-growth can be calculated as the fraction of stands older than t_{og} . The stand age distribution in turn depends on the typical recurrence of stand-replacing disturbances (Johnson and Gutsell 1994). If each parcel of land is equally likely to be disturbed in any given year, the age distribution follows a negative exponential distribution. The cumulative probability distribution of stand ages is given by

$$F(t_{sd}) = 1 - \exp(-t_{sd}/t_{di}) \quad 2.1$$

where t_{sd} is the time since the last stand-replacing disturbance, i.e. the forest age in years and t_{di} is the mean disturbance interval in years. The fraction of old-growth, f_{og} , is then calculated as

$$f_{og} = 1 - F(t_{sd} = t_{og}) \quad 2.2$$

Figure 2.7 illustrates how the predicted old-growth fraction depends on the values of the time to reach the old-growth phase, i.e. in this case the pioneer longevity, and the mean interval of stand-replacing disturbances. Onto this response surface of f_{og} we projected a number of exemplary forest types with their specific median values and quartile ranges for t_{og} and t_{di} compiled from a range of studies (for references see legend of Fig. 2.7). Ideally, the estimates of t_{di} include all types of stand-replacing disturbances (fire, wind, insects, etc.). However, such comprehensive estimates were available only for a limited number of studies (Frelich and Lorimer 1991; Lorimer and Frelich 1994; Zhang et al. 1999; Schulte and Mladenoff 2005). For the boreal and tropical forest regions, we had to rely on data on fire return intervals only, which leads to an overestimation of the fractional old-growth area.

The fraction of old-growth predicted by our simple model forest ranges from 92% in the tropical forest of Central Amazonia to less than 1% in light taiga forests of the boreal zone. There is a clear latitudinal trend of an increasing old-growth fraction from boreal to temperate to tropical forests. Within the temperate biome, broad-leaved deciduous forests are predicted to exhibit higher fractions of old-growth (50–70%) than coniferous forests (10–50%). Within the boreal biome, dark taiga forests dominated by spruce and fir species have higher fractions than Canadian light taiga forests dominated by Jack Pine (*Pinus banksiana*) (30% vs <1%; see Chap. 13 by Bergeron et al., this volume, for a more comprehensive analysis of the North American boreal forests). Across the range of chosen forest types there was a significant negative correlation between the disturbance interval and pioneer longevity. The high old-growth fraction in the central Amazon results

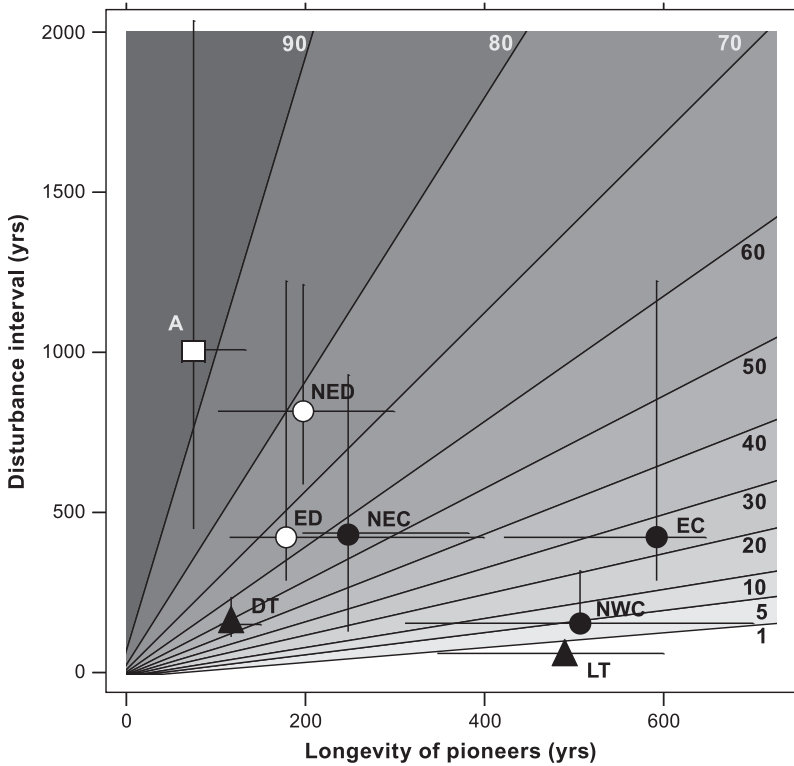


Fig. 2.7 Estimated percentage of old-growth forest under near-natural conditions (*shaded contours*) for a range of forest regions as a function of their characteristic stand-replacing disturbance regimes (y-axis) and the longevity of typical pioneer species (x-axis) as a measure of the time required to reach the old-growth stage. Individual regions: *A* Amazonia, *NWC* western coniferous forests of North America, *NED* eastern deciduous forest of North America, *NEC* eastern coniferous forest of North America, *ED* European deciduous forest, *EC* European coniferous forest, *DT* boreal dark taiga forests dominated by spruce or fir, *LT* boreal light taiga forests dominated by *Pinus banksiana*. Symbol colours indicate whether the late-successional stages are dominated by broad-leaved (*white*) or coniferous (*black*) tree species. Symbol types indicate the biome: *squares* tropical, *circles* temperate, *triangles* boreal. Error bars 20% and 80% percentiles of the literature data. Literature estimates of t_{og} and t_{di} were taken from the following sources: *A* (t_{og} : Laurance et al. 2004; Lieberman et al. 1985; $n = 12$; t_{di} : Sanford et al. 1985; Saldarriago and West 1986; $n = 5$), *NWC* (t_{og} : Burns and Honkala 1990; $n = 18$; t_{di} : Wirth 2005; $n = 12$), *NED* (t_{og} : Burns and Honkala 1990; $n = 32$; t_{di} : Zhang 1999; Lorimer and Frelich 1994; Schulte and Mladenoff 2005; $n = 7$), *NEC* (t_{og} : Burns and Honkala 1990; $n = 11$; t_{di} : Zhang 1999; Schulte and Mladenoff 2005; $n = 13$), *ED* (t_{og} : Ellenberg et al. 1986; $n = 20$; t_{di} : FAO TBFRA 2000; $n = 5$), *EC* (t_{og} : Burns and Honkala 1990; $n = 7$; t_{di} : Burns and Honkala 1990; Wirth 2005; $n = 5$), *DT* (t_{og} : Ellenberg et al. 1986; Nikolov and Helmisaari 1992; $n = 5$; t_{di} : Wirth 2005; $n = 26$), *LT* (t_{og} : Ellenberg et al. 1986; Nikolov and Helmisaari 1992; $n = 6$; t_{di} : Wirth 2005; $n = 28$). Here, n refers to either the number of pioneer species (t_{og}) or the number of stand types or regions used to estimate the disturbance interval t_{di} .

from a combination of very long natural disturbance intervals (>1,000 years) and the occurrence of short-lived pioneer trees with a mean longevity of 80 years. The other extreme is represented by light taiga forest dominated by *Pinus banksiana*. This species is a pioneer on fresh burns and may live for about 200 years, but the highly flammable forests it forms burn on average every 40–60 years (Lynham and Stocks 1991; Carroll and Bliss 1982). The fraction of old-growth in broad-leaved temperate forests ranges between 50% and 80%, with disturbance intervals and pioneer longevities of about 600 years and 200 years, respectively. The major simplification contained in these calculations is the assumption that each parcel of land is equally likely to be disturbed. In real complex landscapes this is never the case and Chap. 13 by Bergeron et al. (this volume) is devoted to illustrating the consequences of spatial and temporal variability of disturbance regimes for old-growth forests occurring in North American boreal forests. Nevertheless, the broad latitudinal gradient emerging for the three major forest biomes (excluding Savannah woodlands and Mediterranean forests), and the differences between coniferous and deciduous forests within the temperate biome, are probably robust. It is also important to realise that these findings are not dependent on the underlying successional definition of old-growth. Similar patterns would emerge if t_{og} was kept constant to represent a uniform age-threshold. For example, projecting all data points onto a vertical line at $t_{og} = 200$ years in Fig. 2.7 would still result in a latitudinal gradient.

2.4.2 *Spatial Scale*

The scheme of Oliver and Larson (1996) distinguishes only between stand-replacing disturbances and gap creation by single tree mortality. However, late-seral communities are often characterised by intervening partial disturbances, with gap sizes just large enough for successful re-colonisation of pioneer species (Lertzman and Fall 1998). Depending on which disturbance types and sizes are accepted under a given old-growth definition, these may become an important component of old-growth forest landscapes (Runcle 1981) or mark the start of a new secondary succession on patches. The spatial dimension may also become important in highly fragmented landscapes, where the natural course of succession is impeded by dispersal limitation of late successional species (e.g. Tabarelli and Peres 2002).

2.5 Identifying Old-Growth – the Conservation Perspective

According to a remote-sensing-based assessment initiated by Greenpeace, only 23% of the world's forests remain intact (see Chap. 18 by Achard et al., this volume), i.e. are not significantly impacted by humans and thus can be considered

primary forest (cf. Sect. 2.3, and Chaps. 17 and 18, this volume). It is primarily within these 23% of the world's forest area where we can expect to find contiguous parcels of old-growth forests. In the race against forest destruction and conversion, the need for practical solutions to old-growth identification arises for state agencies or non-governmental organisations (NGOs) engaged in forest protection seeking efficient methods to map old-growth forest remnants. Even if an all-encompassing, unambiguous definition was available, this would not necessarily lead to a fast and practical detection method. As shown above, obtaining a good estimate of a forest's age distribution – probably the most valuable type of data with which to identify old-growth conditions – is very labour-intensive and thus prohibitive if large areas are to be screened for old-growth forest. There are basically two options: (1) snapshot inventories of structural measures, and (2) remote-sensing (including aerial pictures). Structural features are easily quantified using standard forest inventory methods for live trees and standing dead trees, and fast methods are available for quantifying deadwood dimensions and stocks (van Wagner 1968). These data can be used to derive indicators of 'old-growthness', which can combine multiple thresholds of structural and successional criteria and weighting factors in a pragmatic way (Spies et al. 1988; Messier and Kneeshaw 1999). These become especially useful if data from more detailed studies are available for calibration. The few general principles depicted in such a rating scheme (relatively old, structure indicating gap-phase dynamics, presence of snags and logs resulting from single-tree mortality events – see the shortlist under Sect. 2.6 below) should hold everywhere, and it should be possible to adjust compositional criteria and dimensional thresholds to capture the variability in species pools², growth rates, gap persistence times and deadwood decomposition rates across the globe. While the use of simple measures is unavoidable for rapid screening, it is the consistent evaluation and interpretation of data that should be of prime concern. Unfortunately, work to harmonise existing old-growth inventories at an international level is yet to be done. For example, large inconsistencies emerged when several national datasets were compiled by the Taiga Rescue Network to quantify the spatial extent of the remaining old-growth forest in the Eurasian boreal zone (Aksenov et al. 1999). In Russia, old-growth forest is defined as "... forests originated through natural successions unaffected by destructive human impact over a significant period of time ...". According to the Scandinavian definition, they are characterised as "... originating through natural succession with a significant contribution of old trees and dead wood often with a multi-layered stand structure ...". Hence, according to the Russian definition every stand unaffected by human activity qualifies as old-growth, whereas the Scandinavian definition is closer to the structural definitions mentioned earlier and is thus more restrictive. As a consequence, in Russian provinces like the Komi Republic the 'old-growth' fraction is in the order of

²See also Chap. 17 by Grace and Meir, this volume, in which they emphasise (Sect. 17.1) that many rainforests have the diagnostic characteristics mentioned above, in that they completely lack human impact. Therefore they distinguish old-growth secondary forests that have much of the general appearance of undisturbed forest, but lack some of the biodiversity.

15%, whereas in Scandinavia it is below 1% – despite the fact that the history, dynamics and composition of the forests are broadly similar. In comparison, remote-sensing-based estimates using satellite imagery are obviously unaffected by regional definitions and can be obtained globally using a consistent automated methodology. However, using satellite imagery it is not possible to identify old-growth forest per se but rather ‘intact’ forest regions with a high likelihood of hosting old-growth forests (see Chap. 18 by Achard, this volume). On a more regional scale, canopy structure can be resolved using aerial pictures, and old-growth forests can be identified based on the fraction and dimension of forest gaps (Piovesan et al. 2005).

2.6 Conclusions and Pragmatic Considerations

In Sect. 2.2 we introduced a range of criteria underlying existing old-growth definitions and highlighted – for heuristic reasons – some problems that arise when such definitions are confronted with methodological constraints as well as the structural and successional diversity one encounters in nature (cf. also Chap. 20, Sect. 20.3, this volume). It was decidedly not our goal to distil yet another ‘better’ definition of old-growth forests. Rather, we agree with Wells et al. (1998) who stated “. . . *that a single, precise definition of old-growth applicable to all forest types is neither possible nor desirable*”. There seems to be an inevitable trade-off between the sharpness of the definition of old-growth and its general applicability. Attempts to identify clear quantitative thresholds after which a given forest succession enters the old-growth stage have failed (Hunter and White 1997). Recently, Spies (2004) presented a highly generic scheme that embraces the high diversity of old-growth forest characteristics with respect to development time, structure, grain size of patches and stability, but which – as is to be expected – does not provide a sharp definition. If we abandon the idea of one universal and unambiguous definition, the long list of criteria in Fig. 2.1 (this chapter) and Table 13.2 in Chap. 13 boils down to a few relative descriptors of true old-growth that are more or less captured by the list of Mosseler et al. (2003): (1) relatively old (existence of large old late-successional tree species with ages close to their life expectancy, and a mean age of half the longevity of the dominating trees), and (2) structural and compositional features witnessing self-replacement through gap-phase dynamics (uneven-aged, regeneration of shade-tolerant species, presence of canopy gaps, large snags and logs in varying stages of decay). Wherever necessary the individual chapter authors have further refined the definition to match their specific cases (Messier et al., Chap. 6, Bauhus et al., Chap. 10, Schulze et al., Chap. 15, Armesto et al., Chap. 16, Grace and Meir, Chap. 17, and Freibauer, Chap. 20).

The literature analysis (Sect. 2.3) has shown that the ecological community seems to converge on preferring the term old-growth over related terms irrespective of the subdiscipline, but important regional differences remain. Recently, a number of reviews dealing with definitional aspects have been published and we can

anticipate that these accounts, together with our book project, will help avoid terminological confusion in future. The renewed interest in old-growth forests, especially in industrialised countries of the northern hemisphere has been sparked by an increasing awareness that land-use change and forest management have almost eradicated old-growth forest. In countries like the United States, Japan, China and European countries, true old-growth forests today make up less than 0.5% of the forest area, whereas the analysis in Sect. 2.4 suggested that under natural disturbance regimes we should expect about 50%. The same analysis has shown that, because of very long natural disturbance intervals and rapid successional change, old-growth conditions dominate in the tropics. Hence, deforestation in the tropics by and large means eradicating old-growth forest. Institutions and NGOs involved in the protection of old-growth or primary forests need fast and efficient survey methods and, given the land-use pressure on the remaining areas, they cannot afford to waste time with the laborious methods required to satisfy scientifically precise definitions (Sect. 2.5). Instead, they have to rely on proxy measures based on forest inventory data or remote-sensing imagery (see Chap. 18 by Achard et al., this volume). However, more detailed regional studies and ground-truth data are required to calibrate such proxies.

The central question pursued in this book is how forests in their late stages of succession differ from younger and/or managed forests in their functioning. The old-growth stage is the last in a series of four fundamental stages of forest development (stand initiation, stem exclusion, understorey reinitiation, old-growth; Oliver and Larson 1996) and thus serves as an important reference point for any analysis on age-related trends. However, there are two main reasons why in this book we do not focus exclusively on the old-growth stage:

1. Data on old-growth forests are generally scarce, especially when it comes to ecosystem processes. If we attempt to provide a comprehensive picture of old-growth forest functioning, we cannot afford to lose information by applying an overly strict definition. Many of the data presented in the following chapters will come from forest stands that are in advanced stages of forest succession, but do not qualify as old-growth in the strict sense. Whenever possible, we will therefore indicate whether the data come from mature, transition old-growth or true old-growth stands.
2. Another reason to adopt a broader definition and include transitional stages is to alleviate the ‘time-axis’ problem. If we want to quantify rates of biomass carbon accumulation or the dynamics of NPP over time, the stands have to be arranged along an absolute time axis. However, it is inherent to the definition of true old-growth forests that signs of the event triggering stand initiation, which are needed to age the stand, have vanished. For example, in a chronosequence study on carbon dynamics in Douglas-fir stands, Janisch and Harmon (2002) were unable to determine the stand ages of old-growth stands and had to assign them an arbitrary high age of 500 years. Thus, including mature and transition old-growth stands of known stand ages gives us a better handle on depicting age-related patterns of important ecosystem functions.

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