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Food and Agriculture
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Продовольственная и
сельскохозяйственная организация
Объединенных Наций

Organización de las
Naciones Unidas para la
Alimentación y la Agricultura

منظمة
الغذية والزراعة
للأمم المتحدة

COMMISSION ON GENETIC RESOURCES FOR FOOD AND AGRICULTURE

Item 3 of the Provisional Agenda

INTERGOVERNMENTAL TECHNICAL WORKING GROUP ON FOREST GENETIC RESOURCES

Seventh Session

Rome, 7–9 March 2023

DRAFT SECOND REPORT ON THE STATE OF THE WORLD'S FOREST GENETIC RESOURCES

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I. INTRODUCTION

1. At its Eighteenth Regular Session in 2021, the Commission on Genetic Resources for Food and Agriculture (Commission) considered the preparation of *The Second Report on the State of the World's Forest Genetic Resources* (Second Report) and took note of the progress made. The Commission requested FAO to present the draft Second Report for review by the Working Group at its Seventh Session and then for consideration by the Commission at its Nineteenth Regular Session.¹
2. This document presents, in its *Appendix*, the draft Second Report for information and comments by the Working Group.

II. STATUS OF PREPARATION

3. The draft Second Report is based on the reports received from countries (67), regional networks (2) and international organizations (2), as well as on the scientific literature and additional information gathered. A total of 59 scientists and experts from 23 countries in Asia, Africa, Europe, Latin America and the Caribbean, North America and Southwest Pacific contributed to the preparation of the draft Second Report, in addition to the FAO staff and consultants.
4. The draft Second Report includes preliminary versions of nine of the 13 chapters. In addition, the foreword, a list of abbreviation and acronyms, and the executive summary are still missing. Additional work is therefore required to complete the draft Second Report and to finalize it for publication. Moreover, all chapters will need to be peer-reviewed and the complete report needs to be further edited to ensure internal consistency and improve readability.

¹ CGRFA-18/21/Report, paragraph 66.

APPENDIX

DRAFT SECOND REPORT ON THE STATE OF THE WORLD'S FOREST GENETIC RESOURCES

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**PART 1: THE CONTRIBUTIONS OF FOREST GENETIC RESOURCES TO
SUSTAINABLE DEVELOPMENT**

[CHAPTER 1. VALUE AND IMPORTANCE OF FOREST GENETIC RESOURCES]

PART 2: STATE OF DIVERSITY IN FORESTS AND OTHER WOODED LANDS

CHAPTER 2. STATE OF FORESTS

2.1. Introduction

At the request of its Members, the Food and Agriculture Organization of the United Nations (FAO) collects, analyses and disseminates information on the status of and trends in the world's forest resources through the Global Forest Resources Assessments (FRAs). The results of the first FRA were published in 1948 and the most recent one was completed in 2020.

While the early assessments focused on timber availability, recent assessments have had a more holistic perspective (FAO, 2018). The assessments have also changed from FAO expert driven exercises into a participatory process. Since 2005, FRAs have relied on country data provided by a well-established international network of officially nominated National Correspondents.

Starting from FRA 2005, FAO has collaborated with other international reporting processes, and organizations involved in the collection of forest-related data. It has also worked with members of the Collaborative Partnership on Forests to improve definitions and streamline reporting. This approach led to the establishment of the Collaborative Forest Resources Questionnaire (CFRQ), which was first used in the preparation of FRA 2015. In consultation with countries and international experts, FAO also reviews, in the beginning of each assessment, the scope to avoid overlaps with other data-collection processes, reduce the reporting burden and assure relevance of the reporting content.

FRA 2020 examined the status and trends of around 60 broad categories (under seven main topics) for the period 1990–2020. The backbone of the assessment was data reported through standardized country reports, which were compiled by the National Correspondents through an online platform. More than 700 experts were directly involved in the process. For the first time, all the data and metadata reported to the process were made available through an online platform for all users in an easy-to-use digital format (FAO, 2020).

In the context of the FRA 2020 process, FAO also conducted a global remote sensing survey with the aim to generate independent, robust and consistent estimates of forest area and its changes over time at global, regional and biome levels. In addition, the survey aimed at strengthening countries' capacities to use remote sensing for forest monitoring. It was a separate effort from the country reporting process and was based on visual interpretation of more than 400 000 samples globally by a network of more than 800 national experts from 126 countries. In addition to confirming many of the results of the FRA country reporting process, the survey produced novel information on drivers of deforestation as well as on several other aspects of forest resources that are not comprehensively covered by the country reporting process (FAO, 2022).

2.2. The extent of forests

The global forest area is about 4.06 billion hectares, which is 31 percent of the total land area (FAO, 2020). Most of the world's forests are found within the tropical biome, which accounts for 45 percent of the global forest area. It is followed by the boreal (27 percent), temperate (16 percent) and subtropical (11 percent) domains (FAO, 2020; see also Figure 2.1). Regarding regional and sub-regional statistics, most forests are found in Europe, including the Russian Federation (25 percent), followed by South America (21 percent), North and Central America (19 percent), Africa (16 percent), Asia (15 percent) and Oceania (5 percent) (Table 2.1).

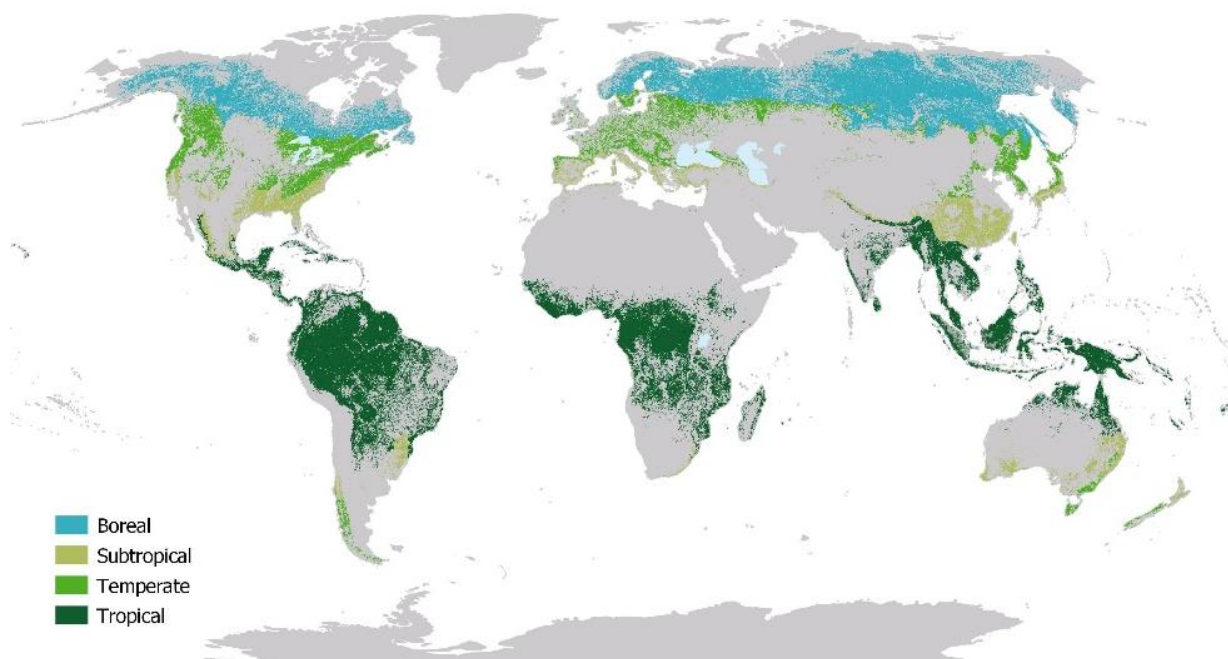


Figure 2.1 The global distribution of forests, by climatic domain. Source: FAO. 2020. *Global Forest Resources Assessment 2020: Main report*. Rome. <https://doi.org/10.4060/ca9825en>

From 1990 to 2020, the total forest area decreased by 178 million hectares (FAO, 2020). The annual rate of net forest loss has decreased from 7.84 million hectares in 1990–2000, to 5.17 million hectares in 2000–2010 to 4.17 million hectares in 2010–2020. Africa reported the highest net loss of forest area (3.94 million ha/y) in the decade to 2020 and was followed by South America (2.60 million ha/y). Asia had the highest annual net gain in forest area in 2010–2020 with 1.17 million hectares. The second largest annual increase for the same period, 348 000 hectares, was recorded for Europe.

While the figures reported above focus on net forest area change, FRA 2020 also collected data on its components – forest expansion (afforestation and natural expansion) and deforestation (conversion of forest to other land uses).

An estimated 420 million hectares of forest was lost globally through deforestation between 1990 and 2020, although the rate slowed over the period (FAO, 2020). Globally, the annual deforestation rate reduced from 15.8 million hectares in 1990–2000 and 15.1 million hectares in 2000–2010, to 11.8 million hectares in 2010–2015 and 10.2 million hectares in 2015–2020.

More than 90 percent of the deforestation during the period 1990–2020 was recorded in the tropical domain where it occurred at a decreasing annual rate from 13.8 million hectares in 1990–2000 compared to 9.28 million hectares in 2015–2020. A significant decrease in annual deforestation was also observed in the subtropical domain where the annual deforestation went down from 1.4 million hectares in 1990–2000 to 0.5 million hectares in 2015–2020.

The regional analysis of the deforestation rates revealed that the highest annual deforestation rate for 2015–2020, 4.41 million hectares, occurred in Africa. It was followed by South America (2.96 million ha) and Asia (2.24 million ha). In Africa, the reported deforestation rate has increased since 1990, while in Asia and South America, it almost halved between 1990 and 2020.

The FRA 2020 findings are complemented by the FRA 2020 Remote Sensing Survey (RSS) that produced information on deforestation by Global Ecological Zones, a subdivision of Global Climatic Domains (FAO, 2022; 2010; see also Figure 2.2).

According to RSS, tropical forests accounted for more than 90 percent of global deforestation in 2000–2018. Most of those losses were recorded for tropical rainforests, where they accounted for 40

percent of the total forest losses in 2000–2018. The Global Ecological Zones with the second and third highest deforestation rates were tropical moist forest and tropical dry forest, which represented 27 and 19 percent, respectively, of global deforestation from 2000 to 2018.

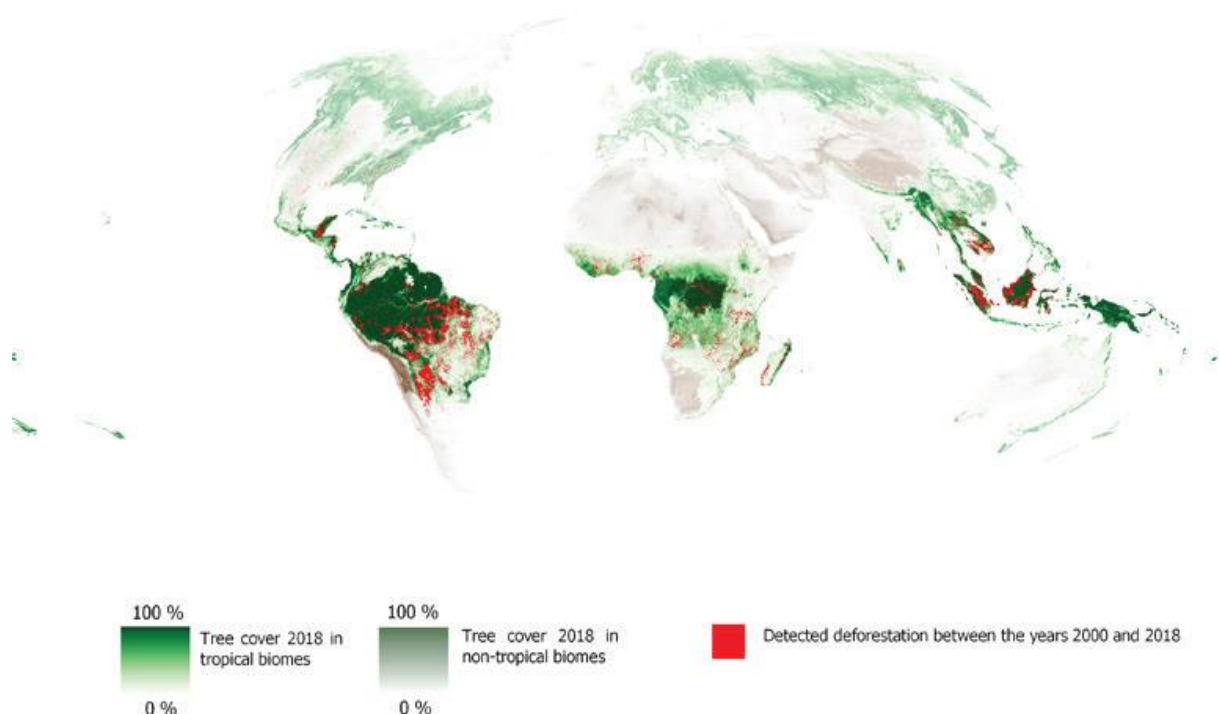


Figure 2.2 Distribution of Remote Sensing Survey samples deforested between 2000 and 2018 in tropical and non-tropical biomes. Source: FAO. 2022. *FRA 2020 Remote Sensing Survey*. FAO Forestry Paper No. 186. Food and Agriculture Organization of the United Nation, Rome, Italy. <https://doi.org/10.4060/cb9970en>

The RSS also analyzed the proportion of forest area deforested since 2000 by ecoregion, a combination of FRA's geographical subregions and Global Ecological Zones (FAO, 2022). This revealed that the tropical ecoregion of Central America had the highest proportion of deforestation between 2000 and 2018. Indeed, 30 percent of forest in the tropical moist ecoregion, and 25 percent of tropical dry forest, rainforest and shrubland ecoregions were lost in Central America in 2000–2018. However, the RSS noted that these boxes should be interpreted with care due to a low number of samples and resulting high sampling errors of the estimates (FAO, 2022).

Table 2.1 Forest area by region and subregion (FAO, 2020).

Region/subregion	Forest area	
	1 000 ha	% of world forest area
Eastern and Southern Africa	295 778	7
Northern Africa	35 151	1
Western and Central Africa	305 710	8
Total Africa	636 639	16
East Asia	271 403	7
South and Southeast Asia	296 047	7
Western and Central Asia	55 237	1
Total Asia	622 687	15
Europe excl. Russian Federation	202 150	5
Total Europe	1 017 461	25
Caribbean	7 889	0
Central America	22 404	1
North America	722 417	18
Total North and Central America	752 710	19
Total Oceania	185 248	5
Total South America	844 186	21
WORLD	4 058 931	100

2.3. Forests characteristics

FRA identifies two broad categories of forest: naturally regenerating forest and planted forest (FAO, 2018). FRA 2020 collected information on both of these categories, as well as on certain subcategories of planted forest (see Figure 2.3).

Naturally regenerating forests account for 93 percent (3.75 billion ha) of the total forest area. Europe has the largest area in this forest category, followed by South America, North and Central America, Africa, Asia and Oceania (Table 2.2).

The area of naturally regenerating forests decreased by 301 million hectares between 1990 and 2020. The overall rate of loss slowed in each ten-year period, from 11.9 million hectares per year in 1990–2000 to 7.84 million hectares in the most recent decade.

Between 2010 and 2020, the area of naturally regenerating forest decreased in all areas except Europe and Oceania. The biggest losses were reported for sub-Saharan Africa, where Angola alone reported an average annual loss of 548 000 hectares in 2010–2020.

The rate of loss of naturally regenerating forests declined by almost half (46 percent) in South America from 5.80 million hectares in 2000–2010 to 3.14 million hectares in 2010–2020. This was mainly due to a reduction in Brazil, where the average annual loss declined from 4.32 million hectares in 2000–2010 to 1.89 million hectares in 2010–2020. While the area of naturally regenerating forest also declined in Asia and North and Central America, the average annual losses in 2010–2020 were significantly lower accounting for 386 000 hectares and 786 000 hectares, respectively. In Europe and Oceania, the area of naturally regenerating forest increased in the same period.

Primary forests are naturally regenerating forests composed of native tree species, and with no clearly visible indications of human activities (FAO, 2018). In these forests, ecological processes are not significantly disturbed. Primary forests – especially primary tropical moist forests – are highly species-rich, diverse ecosystems, and their extent is an important environmental indicator.

The area of primary forests worldwide is estimated at 1.11 billion hectares, or about one-third (34 percent) of the forest area of reporting countries (FAO, 2020). Among the regions, North and Central America has the largest area of primary forest, at 313 million hectares, followed by South America (299 million ha) and Europe (including Russian Federation) (259 million ha). Africa has an estimated 150 million hectares of primary forest, Asia 86.4 million hectares and Oceania 2.62 million hectares.

It should be noted that many countries and territories base their primary forest status and trend estimates on proxies, which reduces the reliability of the findings presented here. Therefore, the results should be treated with caution.

Table 2.2 Annual change in the area of naturally regenerating forest by region and subregion, 1990–2020 (FAO, 2020).

Region/subregion	Average annual change					
	1990–2000		2000–2010		2010–2020	
	Area (1 000 ha/yr)	Rate (%)	Area (1 000 ha/yr)	Rate (%)	Area (1 000 ha/yr)	Rate (%)
Eastern and Southern Africa	-1 351	-0.40	-1 828	-0.57	-1 945	-0.65
Northern Africa	-192	-0.51	-164	-0.46	-182	-0.53
Western and Central Africa	-1 775	-0.51	-1 582	-0.48	-1 887	-0.60
Total Africa	-3 317	-0.46	-3 574	-0.52	-4 014	-0.62
East Asia	835	0.53	473	0.29	776	0.46
South and Southeast Asia	-2 699	-0.90	-889	-0.31	-1 310	-0.48
Western and Central Asia	77	0.17	207	0.44	148	0.31
Total Asia	-1 787	-0.36	-209	-0.04	-386	-0.08
Russian Federation	-239	-0.03	161	0.02	91	0.01
Europe excl. Russian Federation	257	0.22	-7	-0.01	-3	0.00
Total Europe	18	0.00	155	0.02	87	0.01
Caribbean	83	1.42	46	0.71	27	0.40
Central America	-224	-0.83	-225	-0.91	-142	-0.62
North America	-1 099	-0.16	-439	-0.06	-671	-0.10
Total North and Central America	-1 240	-0.17	-618	-0.09	-786	-0.11
Total Oceania	-264	-0.15	-303	-0.17	391	0.22
Total South America	-5 338	-0.57	-5 795	-0.65	-3 135	-0.37
WORLD	-11 928	-0.30	-10 345	-0.27	-7 843	-0.21

Note: The rate of change (%) is calculated as the compound annual change rate.

FRA 2020 estimated the total area of planted forests at 294 million hectares, which is seven percent of the global forest area. Asia has the largest area of planted forest, 135 million hectares. It also holds largest planted forest share, 22 percent, of the total forest area. In Europe, seven percent of forests are planted whereas in Africa and South America only 2 percent of forests are planted.

Globally, the area of planted forests increased in all regions and by 123 million hectares between 1990 and 2020. The average annual rate of increase peaked in 2000–2010, at 5.13 million hectares, while in 1990–2000, it was 4.06 million hectares and 3.06 million hectares in 2010–2020 (Table 2.3).

Most of the increases in planted forest in 2010–2020 were reported in Asia, even though the average annual rate of gain was substantially less in that region than in previous decade. This mainly reflected a decrease in the rate of gain in East Asia, especially China, which reported an annual increase in planted forest of 1.85 million hectares in 2000–2010 and 1.14 million hectares in 2010–2020.

The planted forest category was further divided into plantation forest and other planted forest (Figure 2.3). Globally, there are 131 million hectares of plantation forests, which represent 45 percent of the

total planted forest area. The remainder (55 percent) is categorized as other planted forest, covering 163 million hectares.

The highest share of plantation forests is found in South America, where this subcategory constitutes about 99 percent of the total area of planted forests. Plantation forests also account for most (91 percent) of the total planted forest area in Oceania, about two-thirds (67 percent) in Africa, and more than half (59 percent) in Asia. Other planted forests predominate in Europe, accounting for 94 percent of the total planted forest area, and in North and Central America, at 68 percent of the total.

The area of plantation forests worldwide increased by 55.8 million hectares between 1990 and 2020, with the biggest jump (21.2 million ha) occurring between 2000 and 2010. The average annual rate of gain increased from 1.98 million hectares in 1990–2000 to 2.12 million hectares in 2000–2010 before falling back to 1.48 million hectares per year in the most recent decade.

Globally, the area of plantation forest composed of introduced species was estimated at 49.7 million hectares in 2020, which was 1.4 percent of the total forest area of the reporting countries. Introduced species accounted for 44 percent of the total area of plantation forest in the reporting countries. The largest area of plantation forest composed of introduced species was in Asia, at 20.9 million hectares (32 percent of the total area of plantation forest in that region), followed by South America, at 17.8 million hectares.

The area of other planted forest increased by 66.8 million hectares between 1990 and 2020. The average annual rate of gain increased from 2.08 million hectares in 1990–2000 to 3.01 million hectares in 2000–2010 before dropping to 1.59 million hectares in 2010–2020.

Table 2.3 Annual change in the area of planted forest by region and subregion, 1990–2020 (FAO, 2020).

Region/subregion	Planted forest annual change					
	1990–2000		2000–2010		2010–2020	
	1 000 ha/yr	%	1 000 ha/yr	%	1 000 ha/yr	%
Eastern and Southern Africa	5	0.09	54	0.84	38	0.55
Northern Africa	9	0.66	37	2.27	13	0.70
Western and Central Africa	27	2.54	79	5.07	25	1.18
Total Africa	42	0.48	170	1.76	77	0.70
East Asia	1 082	1.74	1 858	2.44	1 126	1.23
South and Southeast Asia	855	5.20	628	2.59	369	1.25
Western and Central Asia	45	1.14	77	1.70	65	1.23
Total Asia	1 982	2.40	2 563	2.44	1 559	1.23
Europe excl. Russian Federation	483	1.10	551	1.12	292	0.55
Total Europe	754	1.31	976	1.47	219	0.30
Caribbean	2	0.45	23	3.84	12	1.54
Central America	6	6.07	13	7.21	12	3.86
North America	939	3.54	766	2.17	614	1.45
Total North and Central America	947	3.49	802	2.22	638	1.47
Total Oceania	99	3.09	72	1.75	32	0.69
Total South America	236	2.93	546	4.68	538	3.14
WORLD	4 060	2.16	5 130	2.20	3 063	1.11

Note: The rate of change (%) is calculated as the compound annual change rate.



Figure 2.3 Components of planted forest. Source: FAO, 2020.

2.4 The management and ownership of forests

FRA 2020 also collected data on the status of, and trends in, primary designated management objective – that is, the main intended purpose for which a forest is managed and used (Table 2.4). To be considered “primary”, the management objective must be significantly more important than other management objectives, and the forest area reported under a given primary management objective may not be reported under any other primary management objective. However, it should be kept in mind that many forests are managed for multiple purposes and that the primary management objective does not exclude provisions for other benefits or values. For example, sustainably managed naturally generating production forests – for which the primary objective might be wood production – typically also contribute to the protection of soil and water, biodiversity conservation and the provision of social services.

Globally, production of wood and non-wood forest products is the main designated objective (accounting for 28 percent) of the world’s total forest area, followed by multiple use (18 percent). Ten percent of the total forest area is designated primarily for biodiversity conservation and another 10 percent is designated primarily for the protection of soil and water. The provision of social services is the primary designated management objective for 5 percent of the world’s forest area, and “other purposes”, which includes areas of forest managed primarily for scientific research or military and defensive purposes, accounts for another 5 percent. The remaining 23 percent of the world’s forest has no designation or the designation is unknown.

Of the regions, the largest share of forest area designated for production is in Europe, where more than half the forest area is designated for this purpose. If the Russian Federation is excluded, however, the proportion is about 30 percent of the forest area, which is similar to the proportion in North and Central America.

North and Central America and South America have the largest shares of forest area designated for multiple use, and Asia has the largest share of forest area designated primarily for the protection of soil and water.

Forest designated primarily for biodiversity conservation in 2020 was estimated at 424 million hectares, which was 11 percent of the forest area of the reporting countries. The largest area of forest designated for biodiversity conservation was in Africa (107 million ha); this is 24 percent of the total forest area, which is also the highest proportion among the regions. The lowest proportion is in

Europe, at 4 percent, although this increases to 12 percent without accounting for the Russian Federation.

The area of forest designated primarily for biodiversity conservation increased by 111 million hectares between 1990 and 2020, with the largest increase occurring between 2000 and 2010. The rate of average annual increase grew from 3.60 million hectares in 1990–2000 to 5.13 million hectares in 2000–2010, but then dropped by more than half in 2010–2020, to 2.34 million hectares.

The global trend was evident in all regions except Europe and South America, where the rate of increase decreased in each successive decade between 1990 and 2020. The biggest increase in the area of forest designated primarily for biodiversity conservation between 1990 and 2020 was in North and Central America, at 27.4 million hectares, followed by Asia, at 26.1 million hectares, and Europe, at 20.6 million hectares. The biggest increases between 1990 and 2020 in the proportion of total forest area designated primarily for biodiversity conservation were in Africa, from 18 percent to 24 percent, and Oceania, from 11 percent to 17 percent.

The area of forest designated for biodiversity conservation is directly linked to the establishment of protected areas, as these are areas identified as important for the long-term conservation of nature, and managed for that purpose (Dudley, 2008)

In FRA 2020, countries were requested to provide information on the area of forest in formally established protected areas corresponding to International Union for Conservation of Nature (IUCN) protected-area categories I–IV (Dudley, N. and Phillips, A., 2006). In addition, the area and proportion of forests with long-term management plans that are documented and periodically revised, was collected. These two attributes are also components of Sustainable Development Goal indicator 15.2.1 (“progress towards sustainable forest management”), which is reported annually by FAO to the United Nations Statistics Division.

The total area of forest in legally protected areas was estimated at 726 million hectares (18 percent of the total forest area in reporting countries and territories). The proportion of forest in protected areas is more than 30 percent in South America; 11 percent in North and Central America; and 6 percent in Europe. The relatively low proportion of forest in protected areas in Europe is influenced heavily by the Russian Federation, which reported that 2.3 percent of its forest area was protected; if the Russian Federation is omitted, the figure for Europe rises to about 20 percent.

The time series data received showed that the protected area increased between 1990 and 2020. However, the average annual rate of increase slowed from 10.1 million hectares in 2000–2010 to 2.83 million hectares in 2010–2020.

FRA 2020 also collected information also forest management plans, forest ownership and management rights. More than 2 billion hectares of forest is subject to management plans. Almost half of this area is in Europe and particularly in the Russian Federation. Less than 25 percent of the forest area in Africa and South America is under management plans. The area of forest subject to management plans increased by 233 million hectares between 2000 and 2020.

Table 2.4 Six broad management objective categories explained (FAO, 2020).

1. Production	The management objective is the production of timber, fibre, bioenergy and/or non-wood forest products.
2. Protection of soil and water	The management objective is the protection of soil and water.
3. Conservation of biodiversity	The management objective is biodiversity conservation. This category includes but is not limited to areas designated for biodiversity conservation in protected areas.

4. Social services	The management objective is the provision of social services such as recreation, tourism, education, research and the conservation of cultural or spiritual sites.
5. Multiple use	The management objective is a combination of several purposes, none of which is significantly more important than another. Thus, a designation of multiple use indicates that the forest is managed for any combination of production, soil and water protection, biodiversity conservation and the provision of social services.
6. Other	The management objective is other than production, the protection of soil and water, biodiversity conservation, social services or multiple use.

Seventy-three percent of the world's forests is under public ownership, 22 percent is privately owned, and the ownership of the remainder is categorized as either "unknown" or "other" (the latter mainly comprising forests where ownership is disputed or in transition). Public ownership is predominant in all regions and most subregions. Of the regions, Oceania, North and Central America and South America have the highest proportions of private forests. Globally, the share of publicly owned forests has decreased since 1990 and the area of forest under private ownership has increased.

Public administrations hold management rights to 83 percent of the publicly owned forest area globally. Management by public administrations is particularly predominant in South America, where it accounts for 97 percent of management responsibility in publicly owned forests. The share of public administration management rights has decreased globally since 1990, with an increasing share of publicly owned forests managed by business entities and institutions and by indigenous and tribal communities.

2.5. Drivers of deforestation and forest degradation

The drivers of deforestation and forest degradation can be direct or indirect. Direct drivers are identifiable, place-based and visible. Indirect drivers are the underlying driving forces, such as economic, political and cultural factors that result in direct drivers (IPCC, 2022).

Examples of direct drivers of deforestation include conversion of forest into cropland, infrastructure or mines. In the case of conversion to cropland, the underlying indirect driver could be an increase in consumption of meat. That in turn would increase demand and price of soy as feed, which would make conversion of forests into cropland profitable for the landowner.

Direct drivers of forest degradation include, for example, repeated forest fires and long-term overharvesting. The underlying indirect drivers could relate to conflicts in land use (fires) and high demand for charcoal (overharvesting).

RSS found that globally, between 2000 and 2018, almost 90 percent of direct drivers of deforestation were related to agricultural expansion (FAO, 2022). More than half (52.3 percent) of deforested land was converted to cropland and 37.5 percent was used for livestock grazing. Globally, approximately seven percent of deforestation between 2000–2018 was due to oil-palm plantations alone.

The direct drivers of deforestation vary between the regions. In Africa and Asia, more than 75 percent of deforestation was driven by cropland expansion. In South America and Oceania, the most important driver was livestock grazing and in Europe, the land use conversion was dominated by infrastructure and urban expansion.

The extent of forest degradation is more challenging to quantify in the lack of commonly agreed criteria for its assessment. For FRA 2020, 58 countries representing 38 percent of the global forest

area reported that they monitored the area of degraded forest. However, they used varying definitions of degraded forest and few applied quantitative criteria.

At least two recent studies suggest that forest degradation is increasing and even surpassing deforestation rates in certain areas (IPCC, 2022; Matricardi *et al.*, 2020; Sedano *et al.*, 2021; Lapola *et al.*, 2023). Similarly to deforestation, the drivers of forest degradation vary by region. In Africa, charcoal production and wood fuel consumption have been listed as the most important drivers, whereas in Asia and South America wood extraction dominates forest degradation (Hosonuma *et al.*, 2012).

2.6. Conclusions

Regardless of the internationally agreed targets to halt deforestation, restore degraded forest and increase forest area (UN, 2015; UN, 2017), deforestation and forest degradation continue at alarming rates. The reduction in the rate of deforestation and the increase in the area of forests under long-term management plans and within protected areas (FAO, 2020) are signs of gradual improvement towards more sustainable land use, but the speed with which the change is happening, is insufficient.

While the direct drivers of forest loss are mostly related to agricultural expansion, the underlying factors, or indirect drivers, are a complex combination of demographic, economic, political and other factors. Economic growth combined with increasing demand of agricultural products, including timber, weak governance and institutions as well as illegal activities have all been listed among the most important indirect drivers of deforestation (Kissinger *et al.*, 2012).

The world's population has more than tripled since the 1950's and the latest UN projections forecast that it could reach 8.5 billion in 2030, 9.7 billion in 2050 and 10.4 billion in 2100. At the same time, the increasing wealth directs the consumption toward more resource-intensive foods, such as meat and dairy (WRI, 2019). That, combined with climate change, land degradation and biodiversity loss that threaten to decrease the productivity of our food systems, is likely to increase the demand of land for food production.

Halting deforestation, restoring degraded lands and protecting biodiversity require immediate actions to ensure sustainable consumption and production patterns, reduce food loss and waste, develop climate change adapted and mitigating food systems and decouple human economic activity from environmental degradation. As the UN Secretary General said in his remarks to the Security Council in 2018: "We must halt deforestation, restore degraded forests and change the way we farm."²

2.7. References

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CHAPTER 3. STATE OF OTHER WOODED LANDS

3.1. Introduction

The global and local importance of trees outside forests for people and the environment has been increasingly acknowledged in the last decades. Areas with trees, but not meeting the *forest* definition of the Global Forest Resources Assessment (FRA) (FAO, 2018), have been classified in several ways (Box 3.1). Trees in natural woodlands, such as Miombo-Mobane woodlands, are particularly important because globally these lands often correspond with large expanses of dryland. Drylands can be especially vulnerable to climate change, and in them, a diversity of trees provides a particularly crucial role in supporting climate resilience (FAO, 2019a). In a further warming world, understanding the state of trees in dryland systems may therefore hold particular lessons for broader adaptation and mitigation strategies. Areas of agroforestry are also extensive globally, and these areas, often highly diverse in their composition, play a crucial role in supporting rural communities' livelihoods as well as in providing global environmental services (Zomer *et al.*, 2014). The latest State of the World's Forests report (FAO, 2022a) places a particular focus on agroforestry interventions, often as part of 'forest landscape restoration' initiatives, to support planetary health. It states that expanding agroforestry, along with restoring degraded lands, is one of three major interrelated pathways involving trees for supporting both resilient economies and environmental recovery.

In this chapter, the focus therefore is on these trees in natural woodlands and in agroforestry systems. In the following sections of this chapter, both the extent of these lands and the composition of the trees in them is considered. The implications of this information for the management of these lands for conservation purposes, and gaps in knowledge that need to be addressed, are reported.

Trees in urban settings also play a role in supporting livelihoods and biodiversity conservation. Trees in urban setting are not well accounted for in global estimates, but an area of 20 Mha has been reported for urban trees (FAO, 2020). Reported urban trees were mostly in North and Central America, but accounting was incomplete since only 52 out of 236 countries and territories provided information to the report (FAO, 2020). Although this tree category is not covered further in this chapter, we note that cities are aiming to increase urban tree cover in a drive to benefit residents and operate more sustainably (Kowarik *et al.*, 2019).

Box 3.1 Categorising the presence of trees outside forests

When conducting its periodic FRA, FAO asks countries to report on under three headline settings: within *Forest*, within *Other Wooded Land* and within *Other Land* areas (FAO, 2018). Within *Other Land*, FAO uses the *Other Land with Tree Cover* category. In this chapter, capitalisation is applied when referring to these FAO-defined headline categories specifically. This is for the purpose of clarity, as other institutions use the terms differently.

FAO defines Other Land with Tree Cover as "Land classified as "other land", spanning more than 0.5 hectares with a canopy cover of more than 10 percent of trees able to reach a height of 5 meters at maturity." (FAO, 2018). Within Other Land with Tree Cover, for the purpose of FRA reporting FAO recognises trees exclusively within five categories: 1, trees in urban settings (such as parks, alleys and gardens); 2, tree orchards (composed of trees for production of fruits, nuts, or olives.); 3, palms (for production of oil, coconuts or dates.); and 4, agroforestry (agricultural crops and/or pastures/animals) and 5, other (FAO, 2018). Since commodity tree and palm crops, which comprise the second and third of the above setting, are conventionally considered by FAO as *plant* genetic resources, their status is reported in the State of the World's Plant Genetic Resources report.

Nair *et al.* (2022), described agroforestry as involving the growing or retention of trees with crops and/or animals, with major categories of agroforestry systems being termed agrisilvicultural, silvopastoral and agrosilvopastoral. Near-natural extensive systems include shifting cultivation, silvopastoral systems in tropical drylands, silvopasture on former tropical forest land and parkland

systems. Intensive systems include home gardens, smallholder commodity crops and alley cropping (see more information in Box 3.2 below for where these systems are implemented). The near-natural extensive systems in particular are not easily distinguishable, so overlaps in reporting are sometimes to be expected. A key feature of agroforestry systems is the interactions that occur between the different categories of species, such as trees and annual crops, that they contain, which often (although not always) have positive outcomes for livelihoods and the environment (Reed *et al.*, 2017).

3.2. The extent of Other Wooded Land and agroforests

The area extent of Other Wooded Land and agroforests globally has been assessed in different contexts using various methods. A summary of some major studies is provided in Table 3.1, and the data are explained in the following two sub-sections on Other Wooded Land and agroforestry, respectively.

Table 3.1 A summary of data from some major studies on tree extent by geographic region, natural ecosystem and agricultural production system. Data are extracted from the Global Forest Resources Assessment of 2020 (FAO, 2020), the most recent FAO-coordinated remote sensing survey carried out in parallel with the 2020 FRA (FAO, 2022a), the recent FAO-coordinated drylands remote sensing survey (FAO, 2019a) and Zomer *et al.* (2014) agroforestry survey. Other Wooded Land = OWL

Region	FRA 2020 OWL (Mha, to 2020)	RSS OWL (Mha, to 2018)	Drylands RSS ³ OWL in drylands (total, Mha, to 2015) ⁴	Drylands RSS grassland with shrubs within OWL in drylands (Mha, to 2015)	Drylands RSS grassland with trees and shrubs within OWL in drylands (Mha, to 2015)	FRA 2020 agroforestry (Mha, to 2020, for 71 countries) ⁵ . In () is the number of reporting countries	RSS cropland with >10% tree cover (Mha, to 2018, includes oil palm)	RSS grassland with >10% tree cover (Mha, to 2018)	RSS cropland + grassland with >10% tree cover (Mha, to 2018)	Zomer <i>et al.</i> (2014) agricultural land with >10% tree cover (= 'agroforestry', Mha, ave. 2008-2010). In (), in % terms, is the proportion of all agricultural land with >10% tree cover (a, ave. 2000-2002; b, ave. 2008-2010; b minus a ⁶)
North and Central America and the Caribbean ^{7,8}	90.5	341	156.3	110.3	43.1	1.3 (14)	35.1	91.6	126.7	113.7 (46.6; 48.6; 2.0)
South America	146.6	191	52.4	40.2	10.5	0.1 (5)	22.5	133.2	155.7	255.2 (53.0; 65.6; 12.6)

³ The Drylands RSS omitted from calculations large areas of "presumed drylands" in South America, Southern Africa and Central Asia that are on the 'wetter' end of the drylands spectrum.

⁴ Sum of sub-categories tabulated in the report.

⁵ These numbers are given for completeness, but many countries where agroforestry is a major land use did not report or did not fully report figures to FRA 2020.

⁶ Where required, % changes take account of relative area contributions of regions as initially reported by Zomer *et al.* (2014) that are pooled for current reporting.

⁷ Data for 'North America', 'Central America' and 'Caribbean' were (also) given separately in some reports, but summed data are used for current reporting to allow comparison with other studies.

⁸ For Zomer *et al.* (2014) the value given is the sum of the reported regions of 'North America' and 'Central America'.

Europe	100.5	183	10.6	4.2	4.7	0.1 (20)	46.0	92.1	138.1	103.5 (45.0; 45.0; 0)
North Africa ⁹	59.1	39	10.3	3.9	5.5	0.2 (3)	27.1	28.3	55.4	NA ¹⁰
Western and Central Africa	101.9	117	60.9	19.9	26.7	11.2 (6)	124.3	65.8	190.1	NA ¹¹
Eastern and Southern Africa ¹²	284.4	252	128.8	61.2	61.5	1.4 (5)	66.4	105.6	172.0	NA ¹³
Africa total ^{14, 15}	445.5	407	200.0	85.0	93.7	12.8 (14)	217.7	199.7	417.4	120.8 (28.6; 30.5; 1.9)
Asia ^{16, 17}	191.0	208	31.9	10.5	13.3	31.2 (16)	205.4	31.2	236.6	330.4 (40.2; 42.6; 2.4)
Oceania ¹⁸	2.5	370	130.3	64.4	64.0	Negligible (2)	6.6	29.3	35.9	26.3 (30.3; 33.3; 3.0)

⁹ Termed 'Northern Africa' in the Drylands RSS and FRA 2020.

¹⁰ 'North Africa' and 'Western Asia' are reported as a joint figure by Zomer et al. (2014). These data had to be excluded in the current compilation as they are not comparable with categories applied in other reports.

¹¹ Data only reported for 'Sub-Saharan Africa' as a single region by Zomer et al. (2014).

¹² 'Eastern Africa' and 'Southern Africa' were considered separately in the Drylands RSS, but were grouped for current reporting to allow comparison with other studies.

¹³ Data only reported for 'Sub-Saharan Africa' as a single region by Zomer et al. (2014).

¹⁴ For the case of the Drylands RSS the figure reported in the current compilation is the sum of Africa's several individual regions' values (no final sum given for Africa as a whole in the report).

¹⁵ For Zomer et al. (2014) the value given is for the region 'Sub-Saharan Africa' only (i.e., excluding 'North Africa' – see earlier table footnote).

¹⁶ 'Asia' was divided into separate regions in a number of studies, but the country groupings within the regions were not always the same. For current purposes, data were therefore summarised only at the continental level. For the case of the Drylands RSS the figure reported is the sum of Asia's individual regions' values (no final sum given for Asia as a whole in the report).

¹⁷ For Zomer et al. (2014) the value given is for the sum of the individual regional values within Asia, but excludes 'Western Asia' (see earlier table footnote).

¹⁸ Australia did not report under the category of OWL for FRA 2020.

3.2.1. *The extent of Other Wooded Land*

FRA 2020 reported an area of 977 Mha for Other Wooded Land globally leading up to 2020, which equates to approximately 7% of total land area (FAO, 2020). This estimate was around a quarter of the Forest area of 4,059 Mha indicated in the same report. Africa was the continent indicated to have the largest area of Other Wooded Land, with 446 Mha. This was followed by Asia and then South America, both of which were some distance behind Africa in the area revealed, with 191 Mha and 147 Mha, respectively (Table 3.1). The 2020-published FRA also indicated that China, followed by the Russian Federation and then Argentina, were the countries with the greatest area of Other Wooded Land. A decline of 31 Mha in total in the global Other Wooded Land area between 1990 and 2020 was furthermore indicated. The report notes that many countries face challenges in monitoring the area of other wooded land and lack reliable data on them. However, it would appear that FRA reporting reveals that for Africa at least there has been a genuine decline in Other Wooded Land area over the last three decades.

The quality of the data submitted by national partners that forms the basis of FRA reporting varies. Among other factors, it depends on partners' different capacities and capabilities to provide reliable resource estimates, and on how individual nations choose to report. Other factors also affect the ability to compare FRA reporting with alternative data sets of land area extent. For example, FRA reporting is based on a 'land-use' rather than 'land-cover' perspective (FAO, 2018), which can create discrepancies with other data sets.

To help address some of the gaps and discrepancies, FAO supports efforts to better apply remote sensing and modern digital tools for measurements of tree and shrub area extent. The most recent FAO-coordinated remote sensing survey began in 2018 and the work schedule ran in parallel with the preparation of the 2020-published FRA. The remote sensing survey, which was published in 2022, involved over 800 national experts from 126 countries in interpreting satellite images from more than 400,000 geo-located sample sites worldwide (FAO, 2022b). It also used the Open Foris Collect Earth Online image analysis platform that was developed by FAO and its partners (Saah *et al.*, 2019). The survey indicated a total area for Other Wooded Land of 1,701 Mha leading up to 2018, which equates to 13% of total land area. This estimate was almost double that of the last FRA report, a large discrepancy that was not mirrored in the estimates of Forest area of the two reports, which were only a few percentage points apart. The large discrepancy for Other Wooded Land extent may be attributed in part to difficulties in measurement as well as different accounting methods in the country-level reporting behind the FRA figure.

Breaking down the global figure of the above remote sensing survey, Africa, in common with the FRA, was the continent indicated to have the most Other Wooded Land, with 407 Mha leading up to 2018. Oceania, and then North and Central America and the Caribbean (all combined for comparison purposes), followed closely behind, with 370 Mha and 341 Mha, respectively (Table 3.1). The last two regions were indicated to have much greater areas of Other Wooded Land than the FRA had reported. The area indicated as Other Wooded Land was only 91 Mha for North and Central America and the Caribbean in the FRA, while for Oceania it was only 2.5 Mha, a fraction of the area reported by remote sensing. The discrepancy for Oceania is to a large extent explained by the fact that Australia did not provide any data for Other Wooded Land in the FRA 2020 reporting.

Another recent FAO-coordinated remote sensing survey was published in 2019 (FAO, 2019a). This focused specifically on drylands rather than the global situation. Drylands contain large areas of Other Wooded Land that are of particular important from a climate change perspective and are therefore a special focus of attention. Apart from the sampling design, the methods applied in the drylands assessment were similar to those used for the broader global remote sensing survey (FAO, 2022a). The period covered by the drylands study was 2000 to 2015 and images for 213 782 geo-located sample sites were assessed by more than 200 photograph interpreter experts. The assessed drylands covered 41% of the Earth's land surface.

The drylands remote sensing survey indicated that Other Wooded Land accounted in total for 10% of the assessed drylands' land cover, with this proportion higher in semi-arid and arid areas than in hyper-arid and dry subhumid areas. As a proportion of a geographic region's drylands, the survey indicated that Other Wooded Land was mostly found in North and Central America and the Caribbean (considered as a single region), and in Oceania. Both these regions were also indicated to have high dryland Other Wooded Land extents in absolute terms, with 156 Mha and 130 Mha revealed, respectively. Eastern and Southern Africa together, and Africa as a whole, were also reported to have large areas of Other Wooded Land in drylands, with 129 Mha and 200 Mha, respectively (Table 3.1). These data correspond reasonably well in terms of relative regional coverage of Other Wooded Land with the figures reported in the FAO-coordinated 2022-published broader remote sensing survey.

The same drylands remote sensing survey looked at the grasslands in Other Wooded Land areas. These were divided into grassland with shrubs and grassland with both trees and shrubs. These sub-categories covered 54% and 39%, respectively, of the total area of the assessed drylands' Other Wooded Land. The proportions of coverage by these two vegetation types varied by geographic region. For example, while grassland with shrubs was 77% of the reported area of Other Wooded Land in South America, and 71% in North and Central America and the Caribbean (considered together), it was less than 40% in both the region of Western and Central Africa (considered together) and of Northern Africa. In absolute terms, North and Central America and the Caribbean (considered together) was the region indicated to have the most grassland with shrubs within drylands' Other Wooded Land, with 110 Mha. This was followed by Africa with 85 Mha. Africa was the region indicated to have the most grassland with both trees and shrubs within drylands' Other Wooded Land, with 94 Mha. This was followed by Oceania with 64 Mha (Table 3.1).

3.2.2. *The extent of agroforests*

The latest FRA indicated an area of 45 Mha for agroforestry globally (FAO, 2020), but this figure was based on data reported by only 71 countries and is a small fraction of actual agroforestry land (Table 3.1). Many nations with large areas of agroforestry did not report any data on its extent to the latest FRA. Even for those countries that did report extents, the data provided were often incomplete. The scale of under-reporting is illustrated by comparing FRA data with country-level agroforestry area extents approximated as biomass carbon stocks in agricultural lands by Zomer *et al.* (2016). These stocks were highest in Brazil, Indonesia, China, India and the United States of America (USA) (in descending order, 2010 figures). Of these countries, however, only Indonesia, India and the USA reported agroforestry area extents in the latest FRA, and the areas reported in sum for these nations represented only a fraction of known agroforestry areas.

The above-mentioned FAO-coordinated remote sensing surveys (FAO, 2019a, FAO, 2022a) provide more useful insights into the extent of agroforestry. The 2022-published broad remote sensing survey indicated that, leading up to 2018, cropland and grassland globally covered 1,902 Mha and 2,693 Mha, respectively. Of the cropland, 533 Mha (28% of all cropland) was estimated to have tree cover at a level of greater than 10%. The figure for grassland was 577 Mha (21% of all grassland). Africa was the continent reported to have the most cropland with more than 10% tree cover, with 218 Mha (Table 3.1). This was closely followed by Asia, with 205 Mha, and then Europe a distant third, with 46 Mha. Africa was also reported to have the most grassland with more than 10% tree cover, with 200 Mha. This was followed by South America, with 133 Mha. Europe, and North and Central America and the Caribbean (considered as a single region), came about equal third, each with about 92 Mha.

Comparing at a continental level the extents of cropland and grassland with more than 10% tree cover as revealed by the 2022-published broad remote sensing survey, the cropland area was found to be dominant in Asia, while for Africa the area extents were similar (though varying by region within Africa, see Table 3.1). In other regions, the grassland area dominated the cropland area. When combining data for cropland and grassland, Africa had by some distance the largest area of land with at least 10% tree cover, with 417 Mha. This was followed by Asia, with 237 Mha, and then South America, with 156 Mha. The 2019-published drylands survey indicated that 14% of the assessed drylands were cropland and that almost 30% of this cropland had at least some tree cover. Of the

assessed drylands' Other Land (see Box 3.1) as a whole, most land was revealed to have a tree canopy cover of less than 10%.

Other remote sensing surveys have specifically focused on agroforestry area extent and trends. Zomer *et al.* (2014) compared global agroforestry extent for the years 2010 and 2000 using global datasets of tree cover and land use aggregated to a resolution of 1 km². Zomer *et al.* (2014) reported that the highest level of farmland tree cover (as % canopy cover) was found in Southeast Asia, Central America, eastern South America and coastal West Africa. Overall, approximately 1 billion hectares of recognised agricultural land globally were calculated to have more than 10% tree cover in 2010, equating to about 43% of all farmed land. This was an increase in the area of agricultural land with more than 10% tree cover of 3% from 2000 (i.e., increase from 40% to 43%). The figure of one billion hectares with more than 10% tree cover that Zomer *et al.* (2014) calculated is about the same as the combined area of cropland and grassland with more than 10% tree cover that was revealed by the FAO-coordinated 2022-published remote sensing survey (FAO, 2022a), as reported above. Many other areas of agricultural land were indicated by Zomer *et al.* (2014) to have some lesser level of tree cover, with land in Australia, Sahelian nations, Spain and Turkey among notable examples. The extent of these areas was however not fully reported in hectare terms in their study and resolution issues have meant that reliable estimates have been difficult to obtain (but see advances in estimation below).

In a second part of their analysis, Zomer *et al.* (2014) combined maps of tree cover with maps of human population density to estimate how many people lived in agricultural lands with greater than 10% tree cover. Their estimate of 800 million people for 2010 represented a significant proportion of the world's entire rural population. Large concentrations of people living near or in these 'treed' agricultural lands were especially found in parts of Africa and Asia. This pattern was later confirmed by a separate analysis that was conducted for the latest State of the World's Forests report using more recent human population density data (FAO, 2022b).

To support comparisons across regions, Zomer *et al.* (2014) took agricultural land with more than 10% tree cover to equate to agroforestry (though the authors also noted that agroforestry as a system or approach does not align with a specific percentage of tree cover). In these terms, 95% of Central America's agricultural land consisted of agroforests in 2010. For Southeast Asia the figure was 77% and for South America 53%. In absolute terms, Asia had the greatest area of agroforestry in 2010, with 330 Mha reported. This was followed by South America, with 255 Mha. These values surpassed those of other continents in our summary of Zomer *et al.*'s study as compiled in Table 3.1 by at least a factor of two. These data only align partially with the figures reported by FAO in 2022 from the remote sensing survey (tree cover of more than 10% in cropland). Asia featured prominently in both studies, but Africa only featured prominently in the FAO study. In part this is explained by the way data were extracted from Zomer *et al.* (2014) for the purposes of current reporting, where North Africa had to be excluded from the compilation (see footnotes to Table 3.1).

Perhaps most useful from a management perspective, Zomer *et al.* (2014) provided information on how changes in the extent of agroforestry between 2000 and 2010 have varied by geographic region. Comparing 2010 with 2000, South America was observed to have the largest percentage increase in agricultural land covered by agroforestry (considered as more than 10% tree cover). Here, the amount of all farmed land covered by agroforestry was reported to have increased from 53.0% to 65.6% (Table 3.1). Africa, Asia, Oceania, and North and Central America and the Caribbean, also saw decadal increases in the percentage of agricultural land observed to be covered by agroforestry, but Europe did not (no change observed). Within specific continents and regions, opposite trends in agroforestry extent over the decade were sometimes observed. Within an overall Asian figure of an increase of 2.4% for 2000 to 2010, for example, South Asia and East Asia experienced relatively large increases, of 6.7% and 4.9%, respectively, whereas for Northern and Central Asia (considered as a single region) there was a decrease of 2.9%.

Subsequent to 2014, Robert Zomer and his colleagues have focused on exploring the mitigation role of agroforestry in combating anthropogenic climate change. Zomer *et al.* (2016, as already quoted

above), and Zomer *et al.* (2022), started with the same initial data of tree area extent as reported by Zomer *et al.* (2014) and explored global biomass carbon stocks located in agricultural lands. Zomer *et al.* (2016) estimated that these amounted to 45.3 petagrams of carbon (PgC) in 2010, most of which were fixed in trees. Zomer *et al.* (2022) focused on the potential mitigation benefit of increasing tree cover within agricultural systems. They estimated that significant global increases of 4 to 6 PgC of carbon in global biomass stocks could be achieved with incremental changes from current agroforestry practices, while increases of 12 to 19 PgC could be achieved by more substantial systemic changes. South America had the highest potential for extra sequestration, followed by Southeast Asia, West and Central Africa, and North America. The same researchers are currently updating their analyses of agroforestry tree cover and carbon sequestration using improved methods and based on higher resolution datasets that have recently become available (personal communication with Robert Zomer).

3.3. Composition of trees in Other Wooded Land and agroforests

The FAO-coordinated FRAs (e.g., FAO, 2020), remote sensing surveys (e.g., FAO, 2019a, FAO, 2022a) and State of the World's Forests reports (e.g., FAO and UNEP, 2020, FAO, 2022b) noted above summarise data on the area extent of trees in Forest, Other Wooded Land and Other Land. In addition, Zomer *et al.* (2014) specifically addressed the topic of agroforestry extent. These documents say little, however, about the composition of trees in these categories of land cover and how this composition is changing. Nor has determining the composition of trees in Other Wooded Land and in agroforests through systematic inventory, the standard approach that is applied to study composition, received as much attention for these categories of land cover as for trees in Forest, especially not in cross-site comparisons. In the following two sub-sections on Other Wooded Land and agroforestry, respectively, information is presented on how to circumvent this limitation, as well as what is known about composition.

3.3.1. The composition of Other Wooded Land

In the absence of systematic, cross-site inventories for much Other Wooded Land globally, point location data on trees recorded in global databases, such as the Global Biodiversity Information Facility (GBIF, 2022), provide some insights into tree species composition when the geographic co-occurrences of multiple tree species are plotted, especially when taxonomic synonyms can be accounted for and the 'fuzzy matching' of names can be undertaken (Kindt, 2020). These point location data can further be understood in terms of the conservation threats to individual tree species (see elsewhere in this report; Beech *et al.*, 2017; BGCI, 2021). Point location data are however very patchy in coverage globally, with large areas of the world much less sampled than others. This means that they cannot fully inform on composition, individual tree species state and, more importantly, on the drivers of any observed change in state.

In the absence of systematic and comprehensive tree inventory data for many locations, potential natural vegetation (PNV) maps that often focus on the tree component of the vegetation landscape can be a useful proxy for assessing tree species composition. High-resolution PNV maps are most useful. Although globally these are not yet widely available, there are regional exceptions, with Eastern Africa being a good example. Here, the vegetationmap4africa (van Breugel *et al.*, 2015) has been used to characterise landscapes and to prioritise important trees species for woodland restoration. This is in response to overgrazing, overdependence on wood-based energy and the spread of agriculture to marginal lands. The same high-resolution vegetation map, in conjunction with ecological niche modelling and the analysis of molecular genetic diversity datasets for multiple trees species in the Eastern Africa region, has been shown to have practical applications for planning conservation and restoration activities that more fully account for anthropogenic climate change (Dawson *et al.*, 2017).

3.3.2. The composition of agroforests

A wide range of agroforestry systems and approaches are observed globally, some of which are compositionally diverse in the trees they contain (Box 3.2). A limited number of inventories have

been undertaken on tree species diversity in these agroforests, but these studies have not previously been systematically analysed. To address this gap, a systematic literature review of tree diversity inventories in agroforests was conducted as a contribution to the current State of the World's Forest Genetic Resources report.

Box 3.2 Some agroforestry practices in specific geographic regions

Africa: In East and Southern Africa, agroforestry includes cereal-based systems that feature a wide variety of both native and introduced trees valued for timber, fruits, charcoal, fodder and soil-fertility enhancement. In the Sahelian zone of West Africa, traditional parkland systems that are mixed crop-tree-shrub-livestock assemblages derived from savannah ecosystems are important as major sources of food, income, animal browse and environmental services. Farmer managed natural regeneration of trees in the Sahelian zone, which has involved protecting coppice regrowth and wildings during crop establishment, has spread widely in recent decades, increasing local cereal yields. In the humid tropics of West and Central Africa, prevalent agroforestry practices include home gardens and tree commodity crop-based systems. A mix of native and exotic trees are involved, and indigenous fruit trees especially are important sources of human foods. Cocoa agroforests, developed through the modification of lowland tropical forests, depend on the canopy trees to provide shade and cycle soil nutrients within a sustainable, healthy, biodiverse production system. The local trees in these agroforests also provide food, traditional medicine, charcoal and other products, for both household consumption and sale.

Latin America and the Caribbean: Dominant current types of agroforestry include cacao and coffee systems, silvopasture, tree fallows, home gardens, and plantings along field boundaries and contour lines. Both naturally-regenerated native trees, especially for shade and timber, and planted native and exotic trees, are reported in forest landscape restoration initiatives involving agroforestry adoption. Agroforests range from simple designs to complex, highly biodiverse systems such as cabruacas. Here, cacao is planted in cleared understory within native forest and the surrounding trees provide a wide range of products and services beyond shade for the cacao trees, as is the situation also in parts of West and Central Africa (see above). In parts of the Brazilian Amazon, food-producing, soil-fertility-enhancing, medicinal and other useful trees are planted and/or actively encouraged to establish and grow in cassava swiddens.

Oceania: Noted agroforestry practices vary widely. In Australia there is an emphasis on timber production, while on the smaller Pacific islands tree fruits and nuts are important components in intensive farming systems. In Papua New Guinea, native and exotic trees provide important agroecological services, and products for sale and home consumption. Ancient agroforests in the New Guinea Highlands involve trees as windbreaks, soil fertility improvers, and roundwood and fuelwood providers. In the Western Province of Papua New Guinea, gardens of root crops cleared from lowland forest are left to fallow after cultivation and are quickly colonised by native acacia trees that help restore soil fertility. In the Solomon Islands, there has been long-term selection of indigenous fruit and nut trees that are part of traditional agroforests.

Asia: In South Asia, wood-producing commercial agroforestry is important in countries such as India, while fruit orchards and home gardens have key roles in food provision in Bhutan, India and Nepal. Agroforestry practices in South Asia also include silvopastoral systems, coastal shelterbelts, shifting cultivation, tea and coffee production systems, and tree and shrub fodder production. In Nepal, for example, smallholder farmers harvest many different native tree species from agroforests for supplemental fodder for their livestock during the dry winter months. In Southeast Asia, farmers use a rich variety of agroforestry practices, including highly diverse home gardens essential for nutritional security and improved fallows important for broader food security. In some countries in the region, agroforests provide most of the tree-based cash crops. Swidden agriculture in the region, as elsewhere, involves clearing patches in forests to grow staple crops and then abandoning the land for fallow periods. Multistrata agroforests in Indonesia, which are composed mainly of native trees, provide a very wide range of products such as timbers, resins, fruit and barks, as well as important

environmental services including biodiversity conservation, carbon sequestration and water catchment protection. In the Lao People's Democratic Republic and Thailand, agroforests where exotic timber production is combined with grazing, and rice and cassava cultivation, are established in degraded land where primary forest was cut down long ago.

Information summarised from Cornelius *et al.* (2019) and Thomson (2022).

[Editor's note: Final map to be inserted]

Figure 3.1 Summary of findings of a literature review of tree species richness inventories for agroforests. Shown are the results for individual studies from each of 20 nations. Results are tabulated in Annex 3.1, where information on the type of agroforestry system, the number of tree species revealed and the reference to the study are provided. The 'GlobalUsefulTrees' key of the figure indicates the number of useful native tree species for each of the countries sampled in the inventory, according to the GlobalUsefulNativeTrees database (<https://patspo.shinyapps.io/GlobalUsefulTrees/>). The figure shows that there is only a relatively weak correlation between the number of tree species detected in inventories and the number of native species assigned uses in the countries. This suggests that 'benign neglect' may be an important conservation mechanism for trees in agroforests. For details of the literature review, see Box 3.3.

The literature review, which is described in Box 3.3 and summarised in Figure 3.1 (with more information on individual inventories provided in Annex 3.1), revealed the high tree species richness that can be found in agroforests across the tropics and subtropics. This richness reached 424 woody plant species in total in a study conducted by Kehlenbeck *et al.* (2011) in Kenya, which is a figure equivalent to more than 50% of known useful native tree species in the country (though Kehlenbeck *et al.*'s inventory also includes exotic tree species). Overall, the literature review additionally revealed that species richness in agroforests is contributed primarily by native trees, but that exotic trees often dominate on a trees per hectare basis. For example, in a study of coffee farms in Guinea, many native forest trees were found to be represented by a few individuals only in the inventory (Correia *et al.* 2010). Not many of the agroforestry inventories that were identified in the literature review involved longitudinal sampling, but the few studies that did provided evidence for the transition over time for agroforests to less diverse states, which is a concern from a conservation perspective. Sambuichi and Haridasan (2007), for example, found reduced tree species richness and/or a lower proportion of late successional trees, and a higher proportion of exotics, in old compared to new cacao cabruca plantations in southern Bahia, Brazil.

In summary, literature review indicated the high tree species richness of many agroforests and thus, at least at first sight, their potential for tree species conservation. This is supported by the often-positive relationship observed between the tree species diversity found in agroforests and the ecosystem services and livelihood benefits that those agroforests provide, which should be a powerful incentive for farmers to establish and/or maintain this diversity (Reed *et al.* 2017, Ickowitz *et al.* 2022). The observation that many native trees only occur at low densities in agroforests is however problematic for long-term conservation. This is because inbreeding depression may occur for the next generation of these trees if they are poorly connected reproductively, and the trees and therefore the status of the species they represent are vulnerable to the decision-making processes of individual farmers (Dawson *et al.* 2013). Targeted planting and managed natural regeneration that increase the connectivity among rare trees in agroforests may in these circumstances be an important intervention. To support planting where this is a relevant option, improving growers' access to a diversity of tree germplasm that they are interested in planting is a crucial issue that has been well documented but not necessarily acted upon (Lillesø *et al.* 2018; Graudal *et al.* 2021).

Box 3.3 A literature review of tree diversity in agroforests

A review of inventories of tree species richness in the scientific literature was undertaken to provide information on the state of tree diversity in agroforests, using search terms related to 'agroforestry', 'biodiversity' and 'inventory'. The screening of titles and abstracts that were listed in Web of Science and Scopus databases was carried out on 8 May 2022 and revealed an initial set of 150 potentially relevant studies. Full-text screening of each of these studies was then undertaken to determine if each inventory provided a total number of the tree/woody perennial species identified, and if sufficient information on the sampling approach was provided to allow the proper interpretation of findings. Only studies that fulfilled these criteria were taken forward for comparison.

In total, 44 studies from 20 countries passed the full-text screening step. All of these 20 countries were in tropical or subtropical locations, indicating that agroforestry inventory studies are focused within the more biodiverse natural ecoregions globally. For further assessment for this report, for each of the sampled countries the inventory that revealed the greatest tree species richness was chosen and the data summarised visually and through tabulation. A summary of findings for these 20 studies is provided in Figure 3.1, while further information is tabulated in Annex 3.1. The results indicated that a high number of tree species was often found in agroforests.

Detailed assessment of the 20 chosen inventory studies indicated that the diverse sets of trees found in agroforests existed both as planted individuals and as remnants in the landscape, with trees in the last case retained because they have important uses or simply through a process of 'benign neglect'. The trees revealed by inventories were a mix of exotic and native species and were used for a broad range of products and services by local people.

3.4. The management of Other Wooded Land and agroforests

Based on the above major assessments of Other Wooded Land and agroforestry area extents, it is evident that managing trees in both settings is crucial for conserving and facilitating the use of tree genetic resources. Agroforestry lands are often dominated by exotic trees, but many different native tree species are also found and, as already noted, from a conservation perspective, specific interventions are required to support these species. In some agroforestry landscapes that represent modifications of natural ecosystems these native trees dominate. For both Other Wooded Land and agroforestry globally, there are very large area extents of each. In both cases, regional variation in proportional cover, absolute cover, the specific settings of the trees, and the balance between exotic and native species, are also observed. This indicates that tailored interventions are necessary for the management of the trees at regional, national and local scales.

In the case of managing trees in agroforestry settings, a particular contextual issue to consider is the regional and local relationships between changes in agricultural land area and forest cover. For example, while globally almost 90% of the reported deforestation of 93 Mha over the 2000 to 2018 time period was due to agricultural expansion according to the FAO-coordinated 2022-published remote sensing survey (FAO, 2022a; see elsewhere in this report), within this the specific contributors varied by region. In Africa and Asia, the biggest reported contributor was cropland expansion, while in South America most important was the expansion in livestock grazing (together these specific regional expansions in land use type contributed a large proportion of all agricultural expansion globally). Since in Africa agricultural expansion is mostly through smallholder farming, the opportunities for retaining tree cover and associated biodiversity in agroforestry settings may be relatively high, possibly in contrast to in Asia where the expansion in agriculture is often of tree commodity crop plantations, especially of oil palm grown widely in monoculture. The situation in South America may be more akin to Asia in terms of the fewer agroforestry diversification opportunities presented, though the basis of this is very different, with the growth in agriculture driven by large-scale commercial cattle ranching coupled with soybean production (FAO and UNEP, 2020). Although croplands in parts of the tropics constitute areas of high potential for low-cost smallholder-based tree cover restoration, Shyamsundar *et al.* (2022) noted that countries with the most potential often perform relatively poorly for a set of indicators of enabling conditions for smallholder action.

Strengthening these enabling conditions by removing current constraints to action is therefore required. Shyamsundar *et al.* (2022) suggest that partnering with farmers and prioritising their preferences, reducing uncertainty, strengthening markets, and mobilising innovative financing, are key requirements for scaling smallholder-driven restoration.

In the case of Other Wooded Land, future area extent assessments need to be supplemented by more precise and/or more complete ecoregional mapping (see footnotes to Table 3.1; FAO 2019a). Fuller and more consistent reporting in FRA compilations is also required. For agroforestry, particular efforts are needed to integrate this land use more fully into FRA reporting, something that is also required for reporting trees in FAO's Other Land with Tree Cover sub-category more broadly (de Foresta, 2017). This is especially the case where satellite assessment indicates large agroforestry areas exist for non-reporting nations. A simpler-to-correct difference in reporting between various studies that, if addressed, would support comparisons, is to apply standardised definitions to geographic region reporting, as how this is done currently varies by report, even between FAO-coordinated assessments (see footnotes to Table 3.1).

The current absence of adequate national reporting on agroforestry, in this case with reference to climate change mitigation, was attributed by Rosenstock *et al.* (2019) to a combination of institutional, technical and financial challenges. These authors suggest that greater access to remote sensing methods, using consistent definitions, and establishing better practices for cross-institutional collaborations, are among the necessary measures to drive reporting improvements.

3.5. Future prospects

Looking to the future, recent advances in remote sensing using high spatial resolution satellite data and advanced machine learning offer particular opportunities for studying the extent and nature of trees outside of forests. These advances have the potential to improve estimates especially where tree densities are low and for different land use types – say of agroforests compared to orchards and plantations. These methods even provide opportunities to map individual, isolated trees, which have previously been difficult to quantify using remote sensing approaches. The application of these methods to drylands has shown that tree presence can be greater than was first anticipated: for example, this was found to be the case in the West African Sahara and Sahel, where the unexpectedly high values for tree cover observed by advanced remote sensing methods challenged previous notions of desertification (Brandt *et al.*, 2020).

These new approaches, if trained appropriately to specific landscapes with the support of field inventories, provide great potential to gain new insights globally into tree cover in woodlands and croplands, as well as in urban areas. It is expected that, overall, they will show greater tree cover than first anticipated, with concomitant greater planetary health benefits being associated with this non-forest tree cover (Mugabowindekwe *et al.*, 2022). Brandt *et al.* (2020) indicated that the ultimate target of these new methods would be a database that contains information on all trees outside of forests. This information could be further connected to the configurations in which these trees are found, for further management insights (Bolyn *et al.*, 2019).

Advanced remote sensing methods are also becoming more effective at being able to distinguish between tree species and hence provide compositional data. This is easiest for trees with unusual phenologies, such as *Faidherbia albida* in the parkland systems of West Africa (Lu *et al.*, 2022). However, despite advances in methods, it is still expected that longitudinally conducted ground-based inventories will be required to properly identify tree species assemblages, the population densities of individual species, the drivers of change, and the other parameters required to accurately assess levels of conservation and threat, and possible interventions. The absence of longitudinal surveys in tree species richness inventories in agroforests was noted above (see Box 3.3) and addressing this by returning to already studied landscapes to numerate them again could be particularly useful.

The most important advances in devising context-specific sustainable management responses for Other Wooded Land and agroforests will come from a better understanding of the functionality of different landscapes at continental, national and more local scales, for which estimates of tree cover are only one component. This is especially important for understanding how to manage landscapes in response to environmental challenges that require a functional view of differences in vegetation type and composition in particular environmental settings (Aleman and Staver, 2018; Charles-Dominique *et al.*, 2015). Forest and savanna are characterised by different species assemblages and overlap, both with respect to the environments they occur in and with respect to the degree of crown cover, often do not correspond with specific tree cover “cut-offs” as applied by FAO globally to define Forest and Other Wooded Land (van Nes *et al.*, 2018), and in this sense the FAO FRA definitions of land use are not always useful.

3.6. References

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3.7. Annex 3.1

Tabulation of findings of a literature review of tree species richness inventories for agroforests. Shown are the results for 20 nations for which inventory studies fulfilled complete search criteria. For each of these nations, the inventory that revealed the highest tree/woody perennial species richness is provided here (some nations had more than one inventory identified in the review). Studies are listed in order of species richness (lowest to highest). 'Figure label' refers to the key used in Figure 3.1. For details of the literature review, see Box 3.3.

Figure label	Country	Agroforestry system	Inventory results	Reference
A	Côte d'Ivoire	Commodity crop	41 tree species	Herzog (1994)
B	Central African Republic	Parkland	47 tree species	Kpolita <i>et al.</i> (2022)
C	United Republic of Tanzania	Home garden	53 tree species	O'king'ati <i>et al.</i> (1984)
D	Madagascar	Commodity crop	56 woody species	Danthu <i>et al.</i> (2022)

E	Senegal	Parkland	63 tree species	Camara <i>et al.</i> (2019)
G	Ethiopia	Commodity crop	71 woody plant species	Zewdie <i>et al.</i> (2022)
H	Sri Lanka	Home garden	85 tree species	Martin <i>et al.</i> (2019)
J	India	Home garden	87 tree species identified	Das and Das (2005)
K	Guinea	Commodity crop	94 species	Correia <i>et al.</i> (2010)
L	Panama	Silvopasture	99 tree species	Garen <i>et al.</i> (2011)
M	Burkina Faso	Parkland	106 tree species	Bayala <i>et al.</i> (2011)
N	Ghana	Commodity crop	106 shade tree species	Graefe <i>et al.</i> (2017)
P	Mexico	Commodity crop	107 tree species	López-Gómez <i>et al.</i> (2008)
R	Indonesia	Home garden	>120 tree species	Marjokorpi and Ruokolainen (2003)
S	El Salvador	Commodity crop	123 tree species	Méndez <i>et al.</i> (2007)
T	China	Commodity crop	155 shade trees species	Rigal <i>et al.</i> (2018)
U	Costa Rica	Silvopasture	190 tree species	Harvey and Haber (1998)
W	Cameroon	Commodity crop	206 tree species	Sonwa <i>et al.</i> (2007)
Y	Brazil	Commodity crop)	293 tree species	Sambuichi and Haridasan (2007)
Z	Kenya	Home garden	424 woody plant species	Kehlenbeck <i>et al.</i> (2011)

CHAPTER 4. STATE OF DIVERSITY BETWEEN TREES AND OTHER WOODY PLANT SPECIES

4.1. Introduction

Trees evolved over 300 million years ago, and woodiness has since evolved multiple times in plant families across many taxonomic groups (FitzJohn *et al.*, 2014; Kenrick and Crane, 1997). Today's diversity of trees is a reflection of this long history of evolution, with tree species evolving and adapting to different conditions around the world.

As tree-type growth habits have evolved many times across different plant families, there are several definitions of a tree. The tree definition used by IUCN's Species Survival Committee Global Tree Specialist Group (GTSG) is "a woody plant with usually a single stem growing to a height of at least two meters, or if multi-stemmed, then at least one vertical stem five centimeters in diameter at breast height".

The IUCN Red List of Threatened Species (IUCN, 2022) is the most widely used system to assess the probability of extinction for species. In order to assess whether a species belongs to a threatened category (Critically Endangered, Endangered, Vulnerable) the species are evaluated in relation to five criteria: A) Reduction in population size; B) Geographic range; C) Small population size and decline; D) Very small or restricted population; and E) Quantitative analysis of the probability of extinction in the wild (IUCN, 2012). The criteria are based on a set of quantitative thresholds, and if the species are within these thresholds, the species is assessed as threatened – and is at high risk of going extinct. If a species does not qualify for a threatened category now but is likely to qualify in the near future, or if a species is close to qualifying for a threatened category, it is assessed as Near Threatened. Widespread and abundant species are classified as Least Concern, and those species with inadequate information to complete an assessment are assigned Data Deficient. The detailed methodology is presented in the IUCN Red List guidelines (IUCN Standards and Petitions Committee, 2022). The assessments are complemented with a map and additional supporting information including specific distribution, habitat and ecology, population, use and trade, threats and conservation actions.

4.2. Diversity of tree species

4.2.1. Number of tree species

Previous estimates of the global number of tree species have ranged from 45 000 to 100 000 (Beech *et al.*, 2017; Cazzolla Gatti *et al.*, 2022; Fine and Ree, 2006; Oldfield, Lusty, C. and MacKinven, A., 1998; Tudge, 2006). Other reports have suggested that there are 21 000 species in temperate regions (Hunt, 1996) and 40 000–53 000 in the tropics (Slik *et al.*, 2015). GlobalTreeSearch¹⁹, the first global database of tree species and their natural country distributions was published in 2017 (Beech *et al.*, 2017; BGCI, 2022a) and it has been refined continuously ever since. The information in GlobalTreeSearch, derived from a range of plant databases, scientific references and tree experts, is kept up-to-date to reflect changes in taxonomy, nomenclature and life form, as well as known natural distributions of the species. Plant taxonomists and botanists continue to catalogue the diversity of tree species and understand the relationships between species groups. Some areas of the world remain poorly known botanically, and many taxa still remain undescribed.

As of November 2022, there are 58 090 tree species globally (BGCI, 2022a). These tree species are found in 262 different taxonomic plant families and 4 206 different taxonomic plant genera.

Over 45% (26 297) of tree species are found in just ten taxonomic families. The family with the most tree species is Fabaceae with 5 137 tree species, followed by Rubiaceae (4 458), and Myrtaceae (4 176). The most diverse tree genera are *Syzygium* (1 110 species), *Eugenia* (873 species), *Diospyros* (775 species), *Eucalyptus* (734 species) and *Ficus* (709 species).

¹⁹ https://tools.bgci.org/global_tree_search.php

4.2.2. Distribution of tree species

Except for the extreme polar regions and at the Earth's highest altitudes, trees are found in all parts of the world. However, tree diversity is not evenly distributed across the world as species richness (the number of different species) varies between different regions. Tropical tree diversity is higher than that of most temperate regions. For example, Europe has only 465 native tree species (IUCN, 2022; Rivers *et al.*, 2019) and the United States of America (excluding Alaska and Hawaii) has 881 native tree species (Carrero *et al.*, 2022). The tropical continents of Africa (9 388 species), South America (16 581 species) and Asia (18 779 species) have an order of magnitude more species (BGCI, 2022a).

Some tree species are naturally widespread, such as tallow wood (*Ximenia americana*), which is found in 96 countries. However, most tree species have much more restricted distribution ranges limited to a single region or habitat type, and 58% of tree species are single country endemics (BGCI, 2022a).

The country with the most diverse tree flora is Brazil, with 8 758 tree species, followed by Colombia (5 928 spp.) and Indonesia (5 920 spp.) (Figure 4.1; Table 4.1) (BGCI, 2022b). The countries or territories with the most endemic tree species (i.e. species confined to a single country or territory) are Australia, Brazil, China, Colombia, Indonesia, Madagascar, Malaysia, Mexico, New Caledonia, Papua New Guinea and the Philippines. Geographically isolated countries or territories, such as New Caledonia, New Zealand and Madagascar have the greatest proportion of endemic tree species, with over 90% of species being found nowhere else.

[Editor's note: Final map to be inserted]

Figure 4.1 Tree species richness based on natural distribution of all tree species (BGCI, 2021).

4.2.3. Diversity and distribution of useful tree species

Trees play major functional roles in the world's ecosystems and provide a wide range of socio-economic benefits to billions of people (Rivers, 2022) and references therein). Among the many livelihood functions that forests and trees deliver are nutrient-rich foods and incomes for food security (Ickowitz *et al.*, 2022; Rasolofoson *et al.*, 2018). CIFOR-ICRAF have developed the GlobalUsefulNativeTrees database (GlobUNT) (Kindt *et al.*, 2022) by combining native country distribution data from GlobalTreeSearch with information on ten categories of documented human usage available from the World Checklist of Useful Plant Species (WCUPS; Diazgranados *et al.*, 2020). GlobUNT includes 14 014 useful tree species, representing roughly a quarter of the tree species from GlobalTreeSearch and a third of the plant species from WCUPS.

The twenty genera with the highest number of tree species in GlobUNT were *Ficus* (287), *Syzygium* (189), *Diospyros* (184), *Eucalyptus* (155), *Quercus* (117), *Terminalia* (99), *Acacia* (98), *Elaeocarpus* (96), *Garcinia* (96), *Croton* (94), *Prunus* (93), *Coffea* (90), *Pinus* (87), *Salix* (82), *Macaranga* (75), *Dombeya* (74), *Shorea* (74), *Commiphora* (73), *Magnolia* (69) and *Ilex* (67). According to GlobUNT, 9 261 tree species are used as materials and 8 283 as medicines. Moreover, other documented uses include environmental uses (3 317 species), human food (3 310), fuel (2 162), gene sources (1 552), animal food (1 494), social uses (1 396), poisons (1 109) and insect food (712).

Indonesia and Malaysia have the largest numbers of useful tree species, followed by Brazil, China, India and Thailand (Table 4.1). Other countries with high numbers of useful trees include Thailand, Papua New Guinea, Colombia and the Democratic Republic of the Congo. The GlobUNT data also reveals that, in proportion to the total number of native tree species, more species are documented as useful in Africa and Asia as compared to Southern America (Kindt *et al.*, 2022).

Table 4.1 Tree species richness in GlobalTreeSearch (GTS; accessed Nov 2022) and GlobalUsefulNativeTrees (GlobUNT; accessed Nov 2022) for the 23 countries with over 1 000 tree species in GlobalTreeSearch.

Country	Cont ^a	GTS	GlobUNT
Brazil	S-AM	8758	1772
Colombia	S-AM	5928	1342
Indonesia	AS-trop	5920	2724
Malaysia	AS-trop	5402	2115
Venezuela, Bolivarian Republic of	S-AM	4743	1202
China	AS-temp	4584	1594
Peru	S-AM	4554	1106
Ecuador	S-AM	3776	929
Mexico	N-AM	3655	1118
Australia	AU	3246	954
Madagascar	AF	3195	597
Bolivia, Plurinational State of	S-AM	3035	1058
Papua New Guinea	AS-trop	2864	1361
Viet Nam	AS-trop	2630	1205
Panama	S-AM	2625	733
India	AS-trop	2604	1591
Thailand	AS-trop	2573	1478
Costa Rica	S-AM	2547	711
Philippines	AS-trop	2434	1041
Guyana	S-AM	2260	775
Cameroon	AF	2046	1155
Democratic Republic of the Congo	AF	2034	1228
Myanmar	AS-trop	2006	1226

^a Continental distribution according to Brummitt (2001): Africa (AF), temperate Asia (AS-temp), tropical Asia (AS-trop), Australasia (AU), Northern America (N-AM), Southern America (S-AM)

4.2.4. The state of trees

The State of the World's Trees report provides a global overview of the risk of extinction for trees (BGCI, 2021). The report is based on work from the Global Tree Assessment, an initiative to have threat assessments for all tree species available on the IUCN Red List. The Global Tree Assessment, coordinated by Botanic Gardens Conservation International (BGCI) and the Global Trees Specialist Group (GTSG), began in 2015 in recognition of the need to make more information available for tree species, to make more and better informed conservation decisions. The information for the report was compiled using IUCN Red List assessments and other assessments (including national assessments, flora accounts or scientific papers). Of the 58 497 tree species assessed, 142 (0.2%) tree species were classified as extinct and 17 510 (30%) as threatened (BGCI, 2021). A further 13.2% of tree species are recorded as Data Deficient; many of these are only known from small, relatively unexplored areas.

[Editor's note: Final map to be inserted]

Figure 4.2 Number of threatened tree species across the world (BGCI, 2021).

Threatened tree species are found across the world and nearly every country has threatened trees (Figure 4.2). However, the numbers of threatened tree species are not evenly distributed across the

world but follow similar patterns to the species richness maps. The megadiverse countries (Brazil, China, Colombia and Indonesia) have large numbers of both tree species and threatened species. Madagascar also stands out as one of the countries with the highest level of threatened trees (Beech *et al.*, 2021). However, when looking at the number of threatened species in relation to total tree diversity, the pattern is altered. On average, countries have 11% of their trees threatened. Saint Helena (69%, n=11), Madagascar (59%, n=1842) and Mauritius (57%, n=154) are the three countries or territories with the highest proportion of threatened tree species, and of the 15 countries with the highest percentage of threatened tree species, all except Chile are island states or territories (Beech *et al.*, 2021).

4.2.5. Monitoring tree diversity and conservation actions

The GlobalTree Portal is a new tool for monitoring tree species distribution, threats and conservation actions, including *ex situ* and *in situ* conservation status (Beech, Hills and Rivers, 2022; BGCI, 2022b). The data can be accessed on species, country and global levels. It is gathered from the Global Tree Assessment and BGCI's databases (GlobalTreeSearch, ThreatSearch, PlantSearch and GardenSearch). In addition, conservation actions are also being tracked in real time, detailing who is working on the recovery of which species; these can be accessed on the species pages.

As of November 2022, 17 825 (31%) of 58 090 tree species are found in *ex situ* collections (botanic gardens, arboreta and seed banks). Of these, 12 042 species are protected *ex situ* in their country of origin and 13 783 species are protected *ex situ* outside their country of origin. Conversely, 40 265 species are not found in any *ex situ* collections. The situation is somewhat better when it comes to *in situ* conservation, as 34 976 (60%) of 58 090 tree species are found in at least one protected area globally.

4.3. Diversity of woody bamboos

4.3.1. What are woody bamboos?

Bamboos are plants in the grass family Poaceae subfamily Bambusoideae, a single evolutionary radiation of 1 729 species in 130 genera. Bamboos, as we know them today, originated at least 20 million years ago and are the only major lineage of grasses to evolve in association with forests (Clark *et al.*, 2015; Guo *et al.*, 2019). Most bamboos grow along forest edges or in gaps while some occupy the forest understory, although some species have adapted to open habitats such as savannas or high elevation grasslands. Bamboo cultures in Southeast Asia, India, tropical America and elsewhere suggest a long-standing association between bamboos and people (Lucas, 2013).

Most members of the bamboo lineage are woody bamboos: 1 596 species in 106 genera (Vorontsova *et al.*, 2016; POWO, 2021). Their classification and terminology have recently undergone significant change and it is important to note that woody bamboos are defined by their common evolutionary origin and placement in the subfamily Bambusoideae tribe Arundinarieae (temperate woody bamboos) and tribe Bambuseae (tropical woody bamboos). Other superficially similar groups have been classified as bamboos in the past, or are frequently confused with bamboos, including reeds (*Phragmites* and *Arundo*) and ancient forest grasses (e.g., *Anomochloa*, *Puelia* and *Guadella*). Bambusoideae tribe Olyreae (herbaceous bamboos) belong to the bamboos but are not woody (Kellogg, 2015).

Woody bamboos are rhizomatous perennials with woody culms, culm leaves which are distinct from the ordinary pseudopetiolate foliage leaves, foliage leaves with both an inner and an outer ligule, and complex branching with usually more than one branch originating at each culm node. They have a broad variety of inflorescence structures with flowers arranged in either spikelets, like the majority of grasses, or pseudospikelets. The leaves of woody bamboos contain arm cells with well-developed asymmetric invaginations in the cell walls, an anatomical feature unique to the bamboos. Woody bamboos occupy a broad range of environments across the world, largely in tropical to warm temperate ecosystems, with some diversity in cold temperate regions (Clark *et al.*, 2015; Kellogg, 2015).

4.3.2. Evolution and reproductive biology

Ancestors of bamboos were likely broad-leaved tropical forest understory grasses. These evolved to give rise to three modern lineages: herbaceous bamboos, temperate woody bamboos, and the tropical woody bamboos with a neotropical and a paleotropical group (Kellogg, 2015). Debate still surrounds the mechanism of how different ancestral groups became combined to create the woody bamboos, which are all polyploid (Triplett *et al.*, 2014). Proposed mechanisms include ancient hybridisation, allopolyploidy, biased fractionation, genome dominance and diploidisation (Guo *et al.*, 2019; Chalopin *et al.*, 2021).

Woody bamboos are known for cyclical or gregarious flowering where most or all populations of a given species flower at the same time every 10 – 120 years, and frequently all die after seed is produced, often with profound consequences for local ecosystems (e.g., Janzen, 1976; Singleton *et al.*, 2010; Carvalho *et al.* 2013). The drivers behind this unusual flowering are still not understood, but we know that different bamboo lineages evolved at different rates, and presently those with longest flowering cycles are evolving very slowly (Ma *et al.*, 2017).

4.3.3. Temperate woody bamboos

Temperate woody bamboos, comprising approximately 600 species, represent more than one-third of the world's woody bamboo diversity. With their greater tolerance of cold, this is the group commonly seen growing naturally in North America, Japan and Southeast Asia, as well as on tropical mountains (Figure 4.3). They are also widely cultivated in Europe and North America. The majority are “running bamboos” with leptomorph rhizomes, where the apical meristem of the rhizome continues growing laterally while axillary meristems turn upwards to form culms. This generates separate culms, which are further apart, with powerful capacity for lateral spread. They are tetraploid and hybridise easily, so the group includes hybrid genera: the gardening favourite *Pseudosasa japonica* is a hybrid between *Saramorpha* and *Pleioblastus*; *Semiarundinaria* is a hybrid between *Phyllostachys* and *Pleioblastus* (Triplett and Clark, 2021). The most notable genus is *Phyllostachys* with 51 species, easily recognised by tidy paired branches at each branch complement and including *Phyllostachys edulis* (Moso bamboo) grown for building material and edible bamboo shoots (Lucas, 2013; Dixon and Gibson, 2014). The species previously placed in *Arundinaria* and *Yushania* were found to have multiple origins and were separated into smaller genera (e.g., Triplett *et al.*, 2010; Stapleton, 2013; Attigala *et al.*, 2014).

[Editor's note: Final map to be inserted]

Figure 4.3 Distribution of the temperate woody bamboos (source: Bamboo Biodiversity).

4.3.4. Paleotropical woody bamboos

Paleotropical woody bamboos are found in tropical Asia, Africa and Madagascar (Figure 4.4), and consist of approximately 560 species. They have pachymorph rhizomes where the apex of each rhizome turns upwards to produce a culm, usually producing a “clumping bamboo” morphology with multiple culms close together and short swollen rhizomes. Pseudospikelets are common and a number of species produce fleshy fruits, including the spectacular, pear-like fruits of *Melocanna baccifera* (Muli bamboo). The paleotropical woody bamboos are predominantly hexaploid. Many produce large, upright culms utilised for many purposes (Lucas, 2013), but some are slender scrambling or vining bamboos such as *Dinochloa*. The most notable and iconic genera are the widespread *Bambusa* with around 100 species, *Gigantochloa* with 63 species, and *Dendrocalamus* with 41 species including the world's tallest bamboos. Many species of these three genera are widely cultivated in warmer parts of the world.

[Editor's note: Final map to be inserted]

Figure 4.4 Distribution of the paleotropical woody bamboos (source: Bamboo Biodiversity).

4.3.5. Neotropical woody bamboos

Neotropical woody bamboos (Figure 4.5) include approximately 450 species and are morphologically similar to the paleotropical, but tetraploid. This is the least well documented group of woody bamboos, in spite of their diversity and great ecological significance in South and Central America. A new generation of bamboo specialists are now working to fill the gap, and the number of neotropical woody bamboo species is rapidly increasing (Ruiz-Sanchez *et al.*, 2021). *Chusquea* is the largest genus of woody bamboos with just over 200 species and exhibits high rates of morphological diversification into multiple habitats. *Guadua* with 33 species includes the tallest neotropical woody bamboos, as well as the popular timber species *Guadua angustifolia*. Several species of *Otatea* are among the most drought tolerant bamboos in the world (Ruiz-Sanchez, 2015).

[Editor's note: Final map to be inserted]

Figure 4.5 Distribution of the neotropical woody bamboos (source: Bamboo Biodiversity).

4.3.6. Cultivation and naturalisation

Bamboos are commonly known as the “plant of a thousand uses” (Farrelly, 1984). The woody culms are used as “timber” for construction (houses, bridges), furniture, cooking vessels (especially for rice), household items, basketry and many types of handicrafts, musical instruments, charcoal, paper pulp, and poles, among other items, while the young shoots of many species are edible and many species are used in traditional medicine. In more highly processed forms, culms are used to make bamboo laminate, bamboo rayon and bamboo flooring. Both temperate and tropical woody bamboos are also widely grown for landscaping purposes, as specimen plants but also for hedges, privacy screens and windbreaks. Taking advantage of the rhizomatous growth of woody bamboos, a number of species are planted for erosion control or reclamation of disturbed areas.

According to Diazgranados *et al.* (2020), 195 (12%) woody bamboo species have documented uses, primarily for materials, environmental uses, human food and medicine, but collectively are recorded for nine of the 10 assessed categories. Undoubtedly additional species are harvested casually, especially for handicrafts, and not all species known in cultivation are included, so this number surely represents an underestimate. Of the 195 species, 116 (60%) have multiple uses and 50 of these have three or more uses, but only two species, *Bambusa vulgaris* and *Oxytenanthera abyssinica*, have uses recorded for those nine categories. Twenty species are widely cultivated for commercial or environmental purposes (excluding for landscaping) (Table 4.2). Some woody bamboos in the genera *Bambusa*, *Dendrocalamus*, *Gigantochloa*, \times *Phyllosasa* (*Hibanobambusa*), and *Semiarundinaria* are known only from cultivation, with no record of their native origin (Dransfield and Widjaja, 1995; Ohrnberger, 1999).

A total 232 species of bamboo have been recorded as introduced beyond their native ranges, and 12 species were found to be invasive, with *Bambusa* and *Phyllostachys* proportionally the most likely to be both introduced and invasive (Canavan *et al.*, 2016). *Bambusa vulgaris* and *Phyllostachys aurea* are associated with invasions in the greatest number of regions worldwide (Canavan *et al.*, 2016).

In spite of the invasive properties of some woody bamboos, as a practical matter the majority are challenging to cultivate, commonly requiring specialised techniques or species-specific knowledge (Banik, 2015; INBAR Resources). A wide array of insect pests and fungal or viral diseases can cause serious damage in cultivated settings (Shu and Wang, 2015 and references cited therein).

Micropropagation is utilised commercially for a number of commonly cultivated taxa and for *in vitro* flowering, with its potential for facilitating crop improvement (Mudoj *et al.*, 2013; Banik, 2015; Yuan *et al.*, 2017).

Table 4.2 The 20 most commonly cultivated bamboos for commercial/ecological purposes (excluding landscaping). Sources include Benton (2015), Cusack (1999), Diazgranados *et al.* (2020), Dransfield and Widjaja (1995), Lucas (2013 and pers. comm.), R. Saporito (pers. comm.).

Species	Common name	Main uses
<i>Bambusa balcooa</i>	Female bamboo, b(h)eema	Timber, handicrafts, paper pulp, erosion control
<i>Bambusa bambos</i>	Giant thorny bamboo, Indian thorny bamboo	Timber, handicrafts, edible shoots, erosion control
<i>Bambusa blumeana</i>	Thorny bamboo, spiny bamboo, lesser thorny bamboo	Timber, handicrafts, edible shoots, erosion control
<i>Bambusa textilis</i>	Slender bamboo, weaver's bamboo	Handicrafts (especially prized for basketry)
<i>Bambusa tulda</i>	Bengal bamboo, Indian timber bamboo	Edible shoots, paper pulp, timber
<i>Bambusa vulgaris</i> (Primarily the cultivar 'Vittata', but the standard green form is also grown)	Common bamboo	Edible shoots, light construction, paper pulp
<i>Dendrocalamus asper</i>	Giant bamboo, dragon bamboo, rough bamboo	Edible shoots, timber, erosion control
<i>Dendrocalamus brandisii</i>	Velvet leaf bamboo, teddy bear bamboo, sweet dragon bamboo	Edible shoots, timber, handicrafts, furniture
<i>Dendrocalamus giganteus</i>	Giant bamboo, dragon bamboo	Timber, edible shoots
<i>Dendrocalamus latiflorus</i>	Taiwan giant bamboo, sweet bamboo	Edible shoots, light construction, paper pulp
<i>Dendrocalamus strictus</i>	Male bamboo, solid bamboo, Calcutta bamboo	Handicrafts, light construction, paper pulp, charcoal
<i>Gigantochloa apus</i>	Tabasheer or tabashir bamboo, tali bamboo, pring tali, string bamboo	Timber, furniture, handicrafts
<i>Gigantochloa atter</i>	Giant atter, sweet bamboo, black bamboo	Edible shoots, timber, furniture, handicrafts
<i>Gigantochloa pseudoarundinacea</i>	Greater giant bamboo	Timber, furniture, handicrafts

<i>Guadua angustifolia</i>	Colombian timber bamboo, Colombian thorny bamboo	Timber, furniture, handicrafts
<i>Melocanna baccifera</i>	Muli bamboo, berry bamboo	Handicrafts, paper pulp, light construction; fruits are eaten when available
<i>Phyllostachys edulis</i> (= <i>P. pubescens</i>)	Moso, tortoise-shell bamboo	Edible shoots, timber, bamboo fiber and flooring
<i>Phyllostachys reticulata</i> (= <i>P. bambusoides</i>)	Madake, giant timber bamboo, Japanese timber bamboo	Timber, handicrafts, erosion control
<i>Schizostachyum pergracile</i>	Tinwa bamboo	Light construction, cooking vessel, weaving, paper pulp
<i>Thyrsostachys siamensis</i>	Monastery bamboo, umbrella bamboo, Thai umbrella bamboo	Edible shoots, furniture, timber, charcoal, paper pulp

4.3.7. Bamboo conservation

Because bamboos are primarily associated with forest habitats, deforestation is likely the largest threat to bamboo diversity, but good data are lacking. However, most woody bamboos are light tolerant if not sun-seeking, and some species (e.g., *Chusquea* spp. in the Andes) expand their ranges and biomass to occupy disturbed areas and gaps (Judziewicz *et al.*, 1999). While some bamboos are fire-adapted (e.g., *Actinocladum verticillatum* and *Guadua paniculata* in the savannas of South America), most appear to be susceptible to repeated burning. With respect to global climate change, woody bamboo diversity is largely associated with mountain systems (Clark *et al.*, 2015), so warming poses a threat as elevational ranges move upward.

Bamboos in their native distributions appear to reflect the same diversity patterns as in other clades of organisms, that is, relatively few species are common and widespread, a moderate number are moderately common, and the vast majority are rare (Enquist *et al.*, 2019). However, most woody bamboos have not been assessed for the IUCN Red List; this practice has only become standard in more or less the last decade, so data are often available only for newly described or newly revised taxa (e.g., Attigala *et al.*, 2016; Vidal *et al.*, 2023). There are some *ex situ* conservation efforts in the Americas, mainly in Mexico (e.g., the Mexican national bamboo collection, Francisco Javier Clavijero Botanical Garden near Xalapa, Veracruz) and Colombia (*Guadua* living germplasm collection, Juan María Céspedes Botanical Garden near Tuluá, Valle del Cauca). Some botanical gardens in India (e.g., Forest Research Institute Botanical Garden in Dehra Dun, Uttarkhand), China (e.g., Xishuangbanna Tropical Bamboo Garden, Yunnan Province) and Indonesia (see Widjaja, 2019) have significant Asiatic bamboo collections. Virtually all living bamboo collections are located below 1,500 m in elevation, so much bamboo diversity from high elevations in the tropics is not represented in *ex situ* collections. Existing national parks and preserves in bamboo-rich countries nominally protect bamboo diversity across its elevational ranges, but enforcement levels vary, and climate change will continue to disproportionately affect higher elevations.

A wide variety of other organisms are associated with bamboo in its natural habitats, including fungi, insects, and many vertebrates (including bamboo specialists such as pandas and some lemurs) (Judziewicz *et al.*, 1999; Paudyal *et al.*, 2022). Although a large number of fungi and insects are known to use bamboo as a substrate or to eat it, these are not typically problematic in stable natural systems and they contribute to the overall biodiversity of natural bamboo stands (Shu & Wang, 2015).

As the effects of climate change intensify, however, it is to be expected that previously relatively benign fungi or insects could emerge as pests or diseases.

In conclusion, bamboos are unusual among plants, and present multiple challenges for their conservation and use, as well as for research. Superficial similarity between different species in the vegetative state and the common lack of flowering material mean that identification and systematics of bamboos require dedicated specialists with many years of experience. Species description remains incomplete and generic classification is in flux. More research is also needed on the relationships between bamboos and other organisms. In general, the study of bamboo ecology lags behind other aspects of bamboo research (Clark *et al.* 2015).

[4.4. Diversity of rattans and tree-like palms]

4.5. Drivers of change

The drivers of change affecting trees and other woody plant species act in different combinations and at different intensities in different parts of the world, and they also change over time. Afforestation activities primarily utilise exotic, fast-growing tree species and so do not compensate for loss of native species. However, as protection and restoration activities increase, natural and assisted regeneration will increasingly occur.

The main threat to tree species is habitat loss due to the expansion of agriculture, which affects 29% of species, followed by logging and other forms of wood harvesting (27%), livestock farming (14%) and infrastructure development (13%) (BGCI, 2021). Other threats affecting large numbers of tree species include changes in fire regimes, energy production and mining, and also the presence of invasive species. Although climate change currently affects only 4% of tree species that have been assessed, this threat is likely to intensify in future, with trees of island, coastal, dryland and montane ecosystems being the most vulnerable due to a combination of concentrations of rarity/speciation, exposure to changing climate and inability to migrate (Enquist *et al.*, 2019; Tejedor Garavito *et al.*, 2015). Climate change can also interact with other threats, such as fire and the spread of pests and diseases, often intensifying their impacts.

The relative importance of different threats to tree species varies between geographic regions (Rivers *et al.*, 2022). In northern temperate zones (Europe, North America and North Asia), the main threats to tree species are invasive species, pests and diseases, whereas in tropical regions, the main threats are loss of habitat to agriculture (including livestock husbandry) and biological resource use (e.g. logging). Urban and industrial development is a major threat in six different geographic regions, whereas natural system modification, which includes changes to fire regimes as well as ‘reforestation’ with exotic tree species, are important threats in Oceania, Europe and Sub-Saharan Africa (Rivers *et al.*, 2022).

It is also important to note that threats often interact with each other, rather than acting independently. For example, fires may be used to expand the area of agricultural land, which may lead to increased colonisation of non-native species, and development of infrastructure such as roads can open forest areas to other human activities such as logging and livestock husbandry, as well as hunting of wildlife.

[4.6. Conclusions]

4.7. References

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CHAPTER 5. STATE OF DIVERSITY WITHIN TREES AND OTHER WOODY PLANT SPECIES

5.1. Introduction

The conservation of genetic diversity is of global importance. Since 1992, the Convention for Biological Diversity (CBD) has stressed genetic diversity as one of the three pillars of biodiversity to be conserved, describing it as ‘the hidden secret of life’. Recently the 15th Conference of Parties to the CBD announced four goals and 23 targets for achievement by 2030 in the Kunming-Montreal Global Biodiversity Framework, including Target 4:

“Ensure urgent management actions, to halt human induced extinction of known threatened species and for the recovery and conservation of species, in particular threatened species, to significantly reduce extinction risk, as well as to maintain and restore the genetic diversity within and between populations of native, wild and domesticated species to maintain their adaptive potential, including through *in situ* and *ex situ* conservation and sustainable management practices, and effectively manage human-wildlife interactions to minimize human-wildlife conflict for coexistence.” (CBD, 2022).

5.1.1. What is genetic diversity?

The term ‘genetic diversity’ refers to the variation of DNA sequences found within and among individuals, populations, or species. When there are many differences in DNA sequences among individuals, genetic diversity is considered high. When there are fewer differences, then it is considered low. In forest trees (as with all life on Earth), the unique array of DNA sequences belonging to an individual (i.e., its genotype) forms the instructions for developing its physical traits (i.e., phenotype). Broadly speaking, traits are any measurable attribute of an individual (their effect on the individual's fitness may be beneficial, disadvantageous, or entirely neutral). A *functional* trait, on the other hand, is known to influence the fitness and/or performance of an individual. In tree species these may be morphological (e.g., height, diameter at breast height (DBH), leaf area index (LAI)), physiological (e.g., photosynthetic quality, disease incidence) or biochemical (e.g., chlorophyll contents, water use efficiency) (Bian *et al.*, 2022). When genetic diversity of a species or population is high, we expect greater variation for functional traits among its individuals.

New genetic variation arises from genetic mutations, as well as sexual reproduction. A ‘gene’ is a region of DNA that instructs for a particular trait. In forest trees (and all species), it often takes multiple genes combined to provide instructions for a functional trait. Generally speaking, an individual receives two copies of DNA (one from each parent), which includes two copies of every gene along its genome. We refer to these two or more copies of genes as alleles. For any given gene, an individual may have two identical alleles (homozygous) or alternatively, two different alleles (heterozygous). If the individual is homozygous, then they have inherited the same allele from both parents. If they are heterozygous, then they have inherited two different alleles, thus creating opportunities for new traits to emerge. Heterozygosity is mostly advantageous – if there are lots of different versions of a gene (and therefore traits), then natural selection has an assortment to choose from.

Essentially, genetic diversity provides the raw material required for forest trees to adapt to changes in their environment. When novel challenges arise (e.g., pathogenic species or drought), populations with higher genetic diversity are more likely to have alleles (and their associated functional traits) capable of aiding individuals survive the new threat. In a stable environment, high genetic diversity enhances the likelihood that natural selection will purge maladaptive (e.g., those with a negative impact upon fitness) traits in favour of beneficial ones, thus helping a species to improve its performance and adapt to local conditions. A direct positive correlation has been found between genetic diversity and population fitness, with some research finding that genetic diversity can explain up to 19% of fitness variation (Reed and Frankham, 2003). In turn, it follows that populations with

low or declining genetic diversity have fewer opportunities to cope and adapt and are therefore at higher risk of extinction.

Gene flow is a key driving force behind the composition and variance of genetic diversity within a species. Gene flow broadly refers to any mechanism resulting in the movement of genetic variants from one population to another. This may occur through the movement of gametes (i.e., reproductive cells), individuals, or even the migration of entire populations (Slatkin, 1987). A population is generally defined as community within a species where breeding can occur amongst all individuals, but this can be difficult to delineate in forests which often span vast swathes of land.

In forest trees, naturally occurring gene flow mostly arises through movement of seed and/or pollen. When gene flow is high, we would expect higher levels of genetic diversity and lower levels of non-adaptive genetic structure. When gene flow is restricted (e.g., by features in a landscape, habitat fragmentation, pollinator limitation), we expect genetic diversity to decline and/or genetic structure to increase. This is especially true in cases where restrictions to gene flow cause populations to become genetically isolated, that is, no longer exchanging genetic material with neighbouring populations. In some cases, genetic isolation can also lead to unique genetic divergence, resulting in niche local adaptations, genetic distinctiveness, and even speciation.

Essentially, a species' evolutionary and ecological potential relies upon its maintenance of genetic diversity and, if this decreases, it is likely to have reduced adaptive capacity. Therefore, conservation of within species genetic diversity is essential. It can be a critical factor in promoting resilience to future change and may determine a species' survival when faced with the consequences of environmental challenges, habitat fragmentation, and over-exploitation. Poor forest management (e.g., removing too many mature trees from a population) can lead to a decrease in genetic diversity. Understanding these concepts can assist practitioners with management by defining what needs to be conserved or where high-quality germplasm may be sourced (e.g., higher genetic diversity, adaptations to drought).

Some of the key factors which shape gene flow, and therefore the genetic composition of forest tree species, will be discussed in more detail later in this chapter.

5.1.2. Why genetic diversity matters for forest management?

So far, we've looked broadly at the scientific theory underlying our understanding of genetic diversity in natural populations. While these theoretical concepts are applicable to most living organisms, there is a wealth of empirical data that demonstrates their validity in forest tree populations (Griffin *et al.*, 1991). The value of genetic diversity has clear implications for the management of forest genetic resources (Hollingsworth *et al.*, 2020). In a forest management context, the management of genetic diversity in a population can:

- Maintain and enhance population fitness (i.e., survival, growth, and fecundity) and decrease the risk of local extinction.
- Maintain and enhance the variety of different germplasm available for breeders to enhance species traits for economic utilization (e.g., growth rate, timber attributes).
- Maintain and enhance the forest's innate ability to adapt to local conditions and assist future adaptive responses to environmental change (e.g., to climate change, new pests and pathogens).

Furthermore, poor management resulting in the loss of genetic diversity in forests can also have indirect effects on other species in the landscape. For example, genetically determined differences in the morphology and chemistry of individual trees represents a form of habitat diversity for species associated with those trees – from microbes and insects to birds and mammals. Indeed, it is arguable that genetically distinct lineages and varieties reflect an aspect of biodiversity that may warrant conservation in their own right (Coates *et al.*, 2018).

For effective forest genetic resource management, understanding the composition of genetic diversity within species is essential. There are two overarching determinants shaping genetic diversity.

- Population size is directly correlated with the amount of genetic diversity.
- The level of gene flow between populations is directly correlated with genetic structure within a species.

Understanding these allow practitioners to conserve, manage, and harness the genetic variation that occurs within a species. Taking stock of a species' genetic diversity and structure allows practitioners to identify target populations for conservation and restoration, as well as populations with high levels of genetic distinctiveness and local adaptation (which should be protected from introducing non-local material or even be shared with other populations). As such, managing genetic diversity requires a careful balance between preserving beneficial local adaptations while also bolstering resilience to a changing environment (e.g., short-term vs long-term success).

5.2. How genetic diversity is measured and assessed

To manage forest genetic resources, we need to measure, quantify, and monitor the levels of genetic diversity within a species and translate this into a format which can readily be applied to management.

5.2.1. Essential biodiversity variables (EBVs) for genetic diversity

The Group on Earth Observations Biodiversity Observation Network (GEO BON)²⁰ have developed a key set of measurements to study biodiversity change, known as the Essential Biodiversity Variables (EBVs), with a specific set for composition (Hoban *et al.*, 2022).

The four Genetic Composition (EBVs) outlined by GEO BON are:

- *Genetic Diversity*. This can be assessed with both molecular and phenotypic methods. A common molecular method is to compare the proportion of heterozygous and homozygous alleles individuals have within and among populations of a species. It can also be assessed by analysing variance of phenotype across populations and individuals.
- *Genetic Differentiation*. This can be assessed by quantifying and the proportion of genetic diversity and/or phenotypic traits that are different and/or shared between populations within a species (a common molecular metric is F_{st} , in phenotyping analysis the metric Q_{st} is commonly used). The greater the differences in these metrics, the higher the genetic differentiation.
- *Inbreeding*. This can be estimated with molecular methods by comparing the amount of heterozygosity we would *expect* to find in a healthy population under ideal conditions to the amount we *actually observe*. It can also be assessed through pollinations trials which manipulate the relatedness of individuals breeding, or even trigger self-pollination. Inbreeding effect on fitness of the next generation can then be determined by measuring traits such as seed set, seedling establishment, height etc.
- *Effective Population Size (N_e)*. This is the number of individuals required by a population to maintain its levels of genetic diversity over time. This can be complex to calculate and is affected by a multitude of factors (e.g., dioeciousness, overlapping generations). Nevertheless, some 'rules of thumb' have been established. In forest trees, a population size of 500 breeding individuals is considered a minimum effective population size (Hoban *et al.*, 2021).

²⁰ <https://www.earthobservations.org/index.php>

5.2.2. Phenotypic methods for measuring the distribution of genetic diversity within species to guide FGR management

Many tree species can alter their phenotype in response to environmental variables, without this being detectable in genetic variation (known as phenotypic plasticity). For example, research from Western Australia has shown little genetic variation among populations of the species *Eucalyptus marginata* despite there being several subspecies described based upon phenotypic variation (Wheeler *et al.*, 2003). This plasticity is also apparent at the individual level, as shown in *Betula pendula* where a single tree was able to reduce its number of stomata in response to rising CO₂ levels (Wanger *et al.*, 1996).

While modern molecular methods are now widely available (allowing us to analyse and compare genomes), quantitative genetic studies (such as growth trials) have been used to assess forest genetic composition for centuries. Such trials allow forest practitioners to identify which local adaptations and functional traits have a genetic basis. These methods still play an important role in management, such as the selecting of high-quality seed sources.

Common garden trials

Put simply, a common garden trial involves collecting germplasm (e.g., seed, cuttings) from different provenances across a species range (e.g., differing habitats or populations) and growing them under the same (common) conditions within a controlled, experimental setting (e.g., greenhouse, experimental plot). Depending on the design, environmental conditions can be manipulated to suit the purpose of the study to test performance across specific environmental conditions (e.g., by manipulating the precipitation, temperature). Functional traits (e.g., specific leaf area, growth form, phenology, height) can then be measured and analysed. Since individuals are grown under uniform conditions, any differences in these traits likely have a genetic basis. Genetic differentiation can be measured between populations by analysing the difference in quantitative traits (Q_{ST} - e.g., Whitlock, 2008).

Reciprocal transplant trials

Reciprocal transplant trials are used to test and compare the performance of a given set of individuals by growing them within and outside of their local or 'home' environment. Fitness (e.g. height and survival) can be assessed to determine whether there is any evidence of local adaptation (i.e., individuals performing best under local conditions), also known as the home-site advantage. Reciprocal transplant trials can also detect maladaptation to the local environment (when local individuals perform poorly compared to non-local individuals), which is of increasing concern due to climate change. Reciprocal transplant trials can be particularly beneficial for selecting whether to include non-local germplasm as a seed source for a given site (e.g., in sites affected by climate change, testing whether individuals sourced from a site with a hotter/drier climate outperform local individuals).

5.2.3. Molecular methods for measuring the distribution of genetic diversity within species to guide FGR management

Common garden and reciprocal transplant trials are extremely effective at detecting whether the variation of functional traits has an underlying genetic basis. They can also determine the likely success of a given germplasm source, at least in the short term. The downside of these methods is that they are costly and time consuming as forest trees can take decades to reach maturity and yield results (Gibson *et al.*, 2016; Kawecki and Ebert, 2004). However, in what has been a relatively short period of time, molecular methods have become widely available and affordable to researchers. These methods can rapidly analyse genetic composition, and even identify specific genes linked to environmental adaptation. In 2014, the first edition of SoW-FGR summarised the history of molecular methods in FGR. There have been several major advancements since then. Increasing numbers of whole genome sequences for species have been published or are under production, while genomic

technology grows ever cheaper and more accessible (Li *et al.*, 2022; Holliday *et al.*, 2017). Genomics also has increasing relevance to conservation and studies have been used in a range of ways to support this (Isabel *et al.*, 2020). Examples include identifying populations or genes resistant to disease or pests, assessing the adaptive potential of species for climate change, designing frameworks for genetic rescue and/or assisted gene flow operations, analysing populations for levels of genetic diversity (Borrell *et al.*, 2020; Ingvarsson and Bernhardsson, 2020; Isabel *et al.*, 2020; Parent *et al.*, 2020; Isabel *et al.*, 2020).

Since their inception molecular methods have improved in quality, resolution, accessibility, and affordability. Traditionally, allozymes were the main molecular markers used in genetic research but offered limited coverage of the genome. The advent of polymerase chain reaction (PCR) allowed the rapid development of more advanced molecular methods including amplified fragment length polymorphisms (AFLPs), microsatellites, and single nucleotide polymorphisms (SNPs). The field now commonly uses next generation sequencing (NGS), and more recently, whole genome sequencing (WGS) using long-read methods such as Pacbio. These methods sequence millions of small DNA fragments simultaneously, thus drastically reducing the time needed to sequence genomes or parts of many genomes.

The development of reference genomes is also become more common. Effectively, these are ‘ideal’ genomes which provide a representation of the whole genome sequence of a species, which key information such as the location of specific genes. These are constructed from a range of individuals. Reference genomes provide researchers a framework for assembling their genetic data and increase the scope of analyses which aim to identify specific genes under selection.

The first fully annotated tree genome was black cottonwood (*Populus trichocarpa*) in 2006 (Tuskan *et al.*, 2006). Now, there are at least 38 reference genomes of tree species available on public databases (e.g., treegenesdb.org). However, a major challenge in sequencing the whole genomes of forest trees is their variation in size and repetitive regions. For example, gymnosperm genomes can be very large (Scots pine is ~22Gbp) whereas angiosperms tend to have smaller genomes (likely due to genome downsizing in their evolutionary past), such as the pedunculate oak (*Quercus robur*) with a genome size of 1.5Gbp (Pyhäjärvi *et al.*, 2020; Simon and Roddy, 2018; Plomion *et al.*, 2016). Gymnosperm genomes can also have high frequencies of repetitive regions, with Wegrzyn *et al.* (2014) estimating this to be the case for up to 82% of the 22Gbp loblolly pine genome (*Pinus taeda*). Sequencing larger genomes is more resource intensive and therefore more expensive (e.g., the cost of the sequencing itself, but also the skills required to analyse the data), and questions arise over the cost/value ratio when sequencing many repetitive regions.

Coinciding with the increase in the generation of genomic data for tree species, is the need to integrate data into accessible databases. One such example is the TreeGenesDB, which collates genomic, protein, and RNA data on thousands of different species, as well as literature, and provides access to tools and pipelines to interact with and manage data (Wegrzyn *et al.*, 2020; Falk *et al.*, 2018). Users can contribute to the database, but it also sources from repositories such as GenBank. At the time of writing, it houses information across 16 orders, 304 genus, and 2310 species of trees. Such databases help standardise the format of data while increasing accessibility. On top of this, developers are now adding tools and workflows to assist with the analysis of this data (Wegrzyn *et al.*, 2020; Falk *et al.*, 2018). One such tool is the online CartograTree which can analyse TreeGenes data in the context of its geographical location for phylogenetic or population genetic studies (Wegrzyn *et al.*, 2019; Vasquez-Gross *et al.*, 2013).

5.3. Within species attributes shaping genetic diversity

Life history and ecological traits define the levels and structure of genetic diversity within species. These traits interact with forces of environmental change, which further shapes genetic diversity. Consequently, life history traits and both historical (e.g., glacial cycles) and contemporary (e.g., recent habitat clearance) biogeography are critical considerations for planning forest genetic resource management (Table 5.1).

5.3.1. Ecological and life history traits

Life history relates to a species life cycle (e.g., when it reaches sexual maturity) while an ecological trait refers to the interaction of a species with its environment (e.g., preferred habitat). In plant species more broadly, meta-analyses have shown associations between genetic diversity and these traits (Hamrick and Godt, 1996). For example, range size, growth form and mating system can be important predictors of levels of genetic diversity, while growth form, seed dispersal vector and mating system are associated with species-wide genetic structure (Lowe *et al.*, 2018; Broadhurst *et al.*, 2017; Ellegren and Galtier, 2016; Hamrick and Godt, 1996).

Growth habit

Plant species with a larger growth form such as trees tend to live longer and have more overlapping generations over time. This generally leads to trees having reasonably high genetic diversity and some cushioning against genetic diversity loss. That trees are slow growing protects genetic diversity, as it allows individuals to mate across a range of generations and ensures the presence of rare alleles in the gene pool for longer. This is because older trees can harbour genetic diversity which may have otherwise been lost (e.g., from genetic drift due to habitat fragmentation), providing a 'genetic buffering' which supports the maintenance of genetic diversity through generations (Hamrick, 1978).

Range

A range is the geographic area where you would find a species over the course of its lifespan. We can loosely group plant species into categories based on the geographic ranges which they inhabit (Hamrick *et al.*, 1992.) These include (Hamrick *et al.*, 1992):

- *Endemic/localised.* Known from only one or a few populations, in only one locality
- *Narrow.* Found over several to many populations in a relatively restricted area, parts of one or a few countries or political units.
- *Regional.* Found throughout a geographic region or a large portion of a continent.
- *Widespread.* Found throughout a continent or on more than one continental mass.

Forest tree species tend to be wide-ranging and so often span a broad variety of environmental conditions. Therefore, they are likely to display higher genetic variation and diversity across their range, enabling them to adapt and respond to these differing environments. As such, widespread species genetic diversity tends to have higher levels of genetic diversity compared to those with a narrow range. For example, an early study of 332 woody taxa identified significant relationships between woody plants and their life history and ecological traits (Hamrick *et al.*, 1992). On average, endemic/highly localised species had approximately 70% less genetic diversity than widespread species, and over 50% less genetic diversity of the regional/narrow category. Similarly, widespread species had 34% higher genetic diversity than those with a regional/narrow range. Generally, research has continued to corroborate with these early findings. For example, in the restricted species, *Wollemia nobilis* (commonly known as the Wollemi Pine), which only has one known remnant population in a remote canyon of New South Wales, Australia. Only an estimated 89 (46 mature) genetically distinct individuals remain in the wild, all with extremely low genetic diversity and variation (Mackenzie *et al.*, 2022). Conversely, the timber species Scots pine (*Pinus sylvestris*), is one of the most wide-ranging tree species on the planet, spanning across Eurasia. Including plantations, the species is estimated to cover 145 million hectares of Eurasia. Overall, the species has relatively high genetic diversity when compared to less widely distributed taxa, and generally low levels of low genetic differentiation (Pyhäjärvi *et al.*, 2020; Durrant *et al.*, 2016).

Mating system

Plants have complex mating systems which vary between and even within species. These systems can also be influenced by and interact with their environment (e.g., fragmentation limiting mate choice). Mating systems range from complete outcrossing (sexual reproduction with a different individual, often achieved by having male and female flowers on separate individuals) to autogamy (self-pollinating); however, there is a range of intermediate systems (known as mixed mating) between the two (Imai *et al.*, 2016; Schoen *et al.*, 1996). Most forest trees are also able to reproduce clonally (creating near genetically identical offspring), providing alternative reproductive assurance when other options are depauperate (Honnay *et al.*, 2005). As mutations in the DNA (and, as such, new genetic variation), are normally formed and distributed through outcrossing sexual reproduction, genetic diversity tends to be higher in outcrossing species. Of course, mating system selection is a compromise. For example, while clonality and autogamy removes the need to find a suitable mate and thus provides greater reproductive assurance, it comes at the cost of losing the extra diversity introduced by sexual reproduction and outcrossing. Outcrossing, on the other hand, is a key process in the introduction and maintenance of genetic diversity but, this mating system is limited by the availability of potential mates and, depending on the species method of pollination trait of the species, the presence of pollinators. To counteract these issues, plant species - including many tree species - can switch between mating systems, depending on factors such as mate availability or relatedness to mates (Eckert *et al.*, 2010). However, within forest tree species, outcrossing tends to be the preference. For example, a study of 45 neotropical forest tree species found 90% of them to be preferential outcrossers (Lowe *et al.*, 2018). Outcrossing tree species (as many pines are known to be), have been observed to suffer from inbreeding depression when switching to self-pollinating. For example, Douglas fir (*Pseudotsuga menziesii*), when self-pollinating, may see as much as a 90% reduction in seed set compared to when outcrossing (Sorensen *et al.*, 1974). In another example, self-pollinating Scots pine (*Pinus sylvestris*) trees were observed to set 4 times less seed than outcrossing trees (Koelewijn *et al.*, 1999). This is just one example of inbreeding depression, which can manifest in various forms (e.g., reduced seedling survival, reduced height) across life stages.

Pollination and seed dispersal

The way in which a plant disperses its pollen and seed can determine the fundamental level of gene flow possible across a species range (discounting factors that can disrupt or interact with this, which will be discussed below). Essentially, the greater the distance that pollen or seed can travel, the greater the potential for gene flow. While pollen usually has the potential to cross a greater distance than seed and can shape genetic composition, the final destination of the next generation depends on where seed can disperse to and establish itself. Most gymnosperms, including all conifers, are wind pollinated. On the other hand, up to 86% of Angiosperms (flowering trees) are pollinated by animals (Hu *et al.*, 2006), though some major forest tree species which are angiosperms are also pollinated by wind (e.g., many *Quercus* species). Wind and animal/invertebrate pollination form two of the major life history categories shaping genetic diversity. For example, to reproduce through outcrossing, a tree pollinated by wind tends to have far-reaching pollen dispersal but relies on a somewhat random dispersal technique, such as wind patterns (Kling and Ackerly, 2021). Angiosperms, on the other hand, usually have pollinators to transport their gametes to another individual but are limited by their availability and movements. What they do gain, however, is direct transportation of their pollen to the flowers of other individuals. Animal/invertebrate pollinated species can be further subcategorised, with plants pollinated by small invertebrates tending to have restricted pollen dispersal (e.g., bees, flies) and plants pollinated by larger invertebrates and vertebrates tending to have further-reaching pollen dispersal (e.g., birds, mammals).

We can assume similar patterns in the relationship between seed dispersal and gene flow – the greater the potential distance that seed can disperse, the greater the propensity for gene flow across a landscape. Seed dispersal is categorised between species that need a vector to transport their seed, such as attaching to/being eaten by animals (allochory), and those that do not, and instead use gravity or explosive/ballistic mechanisms (autochory). To assess the impact of seed dispersal on the genetic diversity of woody species, Hamrick *et al.* (1992) assessed 322 species using the following categories: gravity, gravity *and* animal-attached, explosive/ballistic, wind, animal-ingested, or animal-attached

only. They found animal ingested seed to be associated with to the highest levels of genetic diversity (and likely gene flow), with wind and gravity dispersal being linked to significantly lower genetic diversity.

5.3.2. Drivers of change

Recent landscape context (e.g., habitat fragmentation, selective logging)

Despite the relative resilience of forests to genetic diversity loss, the clearing and fragmentation of habitats alongside certain logging practices can reduce genetic diversity. Habitat fragmentation results in smaller populations with fewer individuals available to contribute their genetic diversity to the gene pool. On the other hand, selective logging practices which remove too many mature trees may eliminate the ‘genetic buffering’ of overlapping generations (Vranckx *et al.*, 2012; Aguilar *et al.*, 2006; Lowe *et al.*, 2005). Additionally, gene flow is often disrupted between fragmented populations, further limiting mate choice. This can increase the likelihood of mating with relatives (or in some tree species, becoming more likely to self-pollinate or reproduce clonally). Since relatives are more likely to share DNA, this can lead to maladaptive traits appearing in a population due to inbreeding depression.

Evidence also suggests that habitat fragmentation can disrupt pollinator densities and behaviour, reducing opportunities for plant species outcross. This has been shown to increase the likelihood of inbreeding and self-pollination in tree species which rely on pollinators. A study of the impact of habitat fragmentation on the genetic diversity of three eucalypt tree species found that the predominantly bird pollinated species demonstrated lower levels of inbreeding compared to the two insect-pollinated species (Breed *et al.*, 2015). Further, their meta-analysis showed that habitat fragmentation increased the likelihood of these trees self-pollinating; yet species with more mobile pollinators were somewhat less likely to experience this transition (Breed *et al.*, 2015). Given that birds have far greater mobility than invertebrates, this suggests that tree species with higher pollinator mobility may be somewhat shielded against the negative impacts of habitat fragmentation.

Demographic/evolutionary history (e.g., historic range disjunction)

An understanding of historic population dynamics can be used to guide contemporary forest management, such as identifying populations with high genetic diversity to conserve. For example, during ice ages, forest trees became restricted to habitats which were not covered in ice, contracting and expanding their range based upon the available habitat. Range contraction will essentially bring with it the genetic diversity of the surviving population or species, where it will take ‘refuge’ until able to colonise newly available habitat (e.g., when ice thaws). During periods of rapid expansion, not all genetic diversity will disperse at the same rate, and we are still able to detect these areas of ‘genetic refugia’ using molecular methods. Indeed, they still sometimes harbour higher levels of genetic diversity than elsewhere in a species range and can be seen in species such as Scots pine, where diversity is lower outside of refugia in its northern range following expansion (Cheddadi *et al.*, 2006). Other pockets of high genetic diversity can also be found when multiple isolated refugia later expand and meet, resulting in genetic admixture. In an analysis of >20 European trees and shrubs impacted by glaciation, Petit *et al.*, (2003) found the overall most genetically diverse populations more likely to be found in post expansion ‘meeting points’ of glacial refugia.

Characteristics of glacial refugia are also known to influence structure in modern populations: for instance, North American tree species which had larger and more widespread glacial refugia have been shown to exhibit stronger differentiation between populations and subspecies along with higher genetic diversity (Roberts and Hamann, 2015). It is important to note that other factors, such as gene flow barriers like topography, will influence the demographic history of species, and in some cases can be more important for establishing distinct genetic cluster than glacial cycles (Milesi *et al.*, 2023).

An understanding of previous population dynamics can give us a ‘baseline’ for management in the present-day by helping us answer questions such as ‘what is the minimum viable population size to

maintain genetic diversity?', and 'where is a species no longer found and why?'. For instance, a recent study of several European species of forest trees showed that effective population size was maintained (or even increases) during glacial cycles. These results suggest effective population size can be low in trees species, giving them some resilience to (Milesi *et al.*, 2023).

The historical effect of landscape on genetic composition is also important for considering the definition of management units (Moritz 1994). Again, using ice age as an example, analysis of historical demography can help define conservation units within a species. For example, if multiple populations of a species retract to differing habitats, and become isolated from one another for long enough, they may begin separate evolutionary histories due to lack of gene flow. This can lead to unique local adaptations, subspecies, and eventually speciation. This was also noted by Milesi *et al.* (2023) where elevation was associated with increased divergence and which could suggest distinct subpopulations adapted to elevated, cold environments, in line with previous findings (Hirao *et al.*, 2017). An understanding of these evolutionary histories can assist guide the design of seed transfer zones.

Selective pressures from environment and ecological interactions

Multiple factors shape the overall genetic diversity within forest trees. Those previously mentioned can dictate which raw materials (i.e., genetic diversity and associated functional traits) a species has available to interact with the various elements of its environment (e.g., precipitation, temperature, elevation etc) and to cope with a variety of stressors (e.g., pests and disease). These factors then place a selective pressure on the genetic diversity associated with the most desirable functional traits, even with the high levels of gene flow commonly found in forest trees. Indeed, sometimes these selective pressures can be so great that genetic divergence occurs even in the face of gene flow. Greater understanding provides significant contributions to adaptive management of forest trees (Holliday *et al.*, 2019). Breeding programmes are able to select seed sources based upon their associated adaptative tolerances to future climate change scenarios (e.g., heat, drought), or to forest pests and diseases. Ingvarsson and Bernhardsson (2019) combined whole genome sequencing of 94 individuals of European aspen (*Populus tremula*) with phenotypic trait and vegetative fitness analysis across a latitudinal gradient in Sweden. They found the northern populations to be at risk of maladaptation due to climate change in a relatively short period of time (<50 years), thus alerting practitioners to a higher need for genetic management of these populations (such as facilitating gene flow from populations further south). In white spruce (*Picea glauca*) researchers have identified up to nine genes which correlate which chemical mechanisms which defend the species against defoliation by spruce budworm without compromising desirable growth traits, presenting trees with these genes as good candidates for future breeding programmes (Parent *et al.*, 2019).

Table 5.1 Summary of the general patterns of drivers of levels of genetic diversity (GD within plant species), where darker green indicates high levels of expected/predicted diversity; reflecting intermediate levels, and pale red reflects low levels of expected genetic diversity. (adapted from Hamrick et al, 1992, Broadhurst *et al.* 2016, Lowe et al 2017).

DRIVER	PROCESS	GD	CATEGORIES
Ecological and life history traits	Range size	High	<i>Widespread</i>
		Intermediate	<i>Regional</i>
		Low	<i>Endemic/localised</i>
	Mating system	High	<i>Outcrossing</i>
		Intermediate	<i>Mixed</i>
		Low	<i>Self-pollination/clonality</i>
	Gene flow – Pollination/ seed dispersal	High	<i>Long distance</i> (birds/wind)
		Intermediate	<i>Intermediate distance</i> (large invertebrates, vertebrates)
		Low	<i>Restricted</i> (small invertebrate pollination/gravity seed dispersal)
	Gene flow – Longevity/form	High	<i>Long lifespan</i> (>100 years)
		Intermediate	<i>Intermediate lifespan</i> (20-100 years)
		Low	<i>Short lifespan</i> (5-20 years)
Recent landscape context	Gene flow – habitat fragmentation	High	<i>Continuous</i> populations
		Intermediate	<i>Semi-continuous</i> populations
		Low	<i>Highly fragmented</i> populations
Demographic and evolutionary history	Gene flow – Demographic history (e.g., range disjunction)	High	<i>Semi-continuous/continuous</i> populations
		Low	<i>Highly disjunct</i> (major geographic barriers present, e.g., mountain, large river)
Selective pressures from environment	Environmental isolation (e.g., altitude, climate) or ecological pressures (pests, disease).	High	<i>Homogeneous</i> environment (little variation across its geographical range)
		Low	<i>Heterogeneous</i> environment (e.g., spanning the elevation of a mountain, major climatic or soil differences)

5.4. Patterns of genetic diversity of forest trees and other woody species

5.4.1. Biomes

Globally, there are a diverse range of ecosystems across many different habitats, making up the biosphere. Ecosystems are shaped by a range of factors, such as climate and geography, while the flora and fauna themselves also influence the surrounding environment. These characteristics of a region – its species, climate, and geology – are termed its biogeography (Hanson *et al.*, 2012). Studying this across regions therefore provides us with an opportunity to define environments and their characteristics while identifying what drives their formation. This approach can be applied at all levels of ecological organisation, imposing a hierarchy on the ecological structure of the planet (Mucina, 2019). Consequently, we can choose to separate out the biosphere in a finer, more localised way, or in a broader manner (Olson *et al.*, 2001).

While debate, both semantic and scientific, remains over exactly how levels in this hierarchy should be defined, a widely used concept is that of biomes. Though no universal definition exists, a biome is generally described as a relatively large-scale region which covers a portion of a continent, is dominated by a specific plant type (e.g., broad leaf forest, grass, Mediterranean vegetation), and experiences a specific climate and level of rainfall (Mucina, 2019). Biome formation is largely driven by these last two factors, though elements like soil type also influence this (Keith, 2020; Woodward *et al.*, 2004).

Earlier descriptive studies focused on biome climate and precipitation and the way this influenced biome type and the constituent species. More recently, for a variety of reasons, there has been increased interest in genetically defining the plant and animal species in different biomes. Firstly, biomes are dynamic communities which change both spatially and temporally, driving evolution and adaptation. By analysing the constituent species genetic structure, a greater understanding of their (and by extension the environment's) history can be gained (Hu *et al.*, 2020). Secondly, we can assess how biomes influence the genetic diversity and genetic distribution of species, compare this to other regions, and ascertain what is typical, particularly since there will be a variety of species with differing life history and ecological traits (Broadhurst *et al.*, 2017). Finally, this information can be used practically to inform conservation efforts, allowing us to pinpoint populations and species at increased risk of extinction due to low diversity and adaptation potential, or find those with high diversity which can be used to bolster gene pools (Newton *et al.*, 1999). Previous studies have highlighted areas or subpopulations of high genetic diversity worthy of conserving or seed banking, such as Southern African populations of *Acacia* spp. (Lyam *et al.*, 2022). Preserving these is especially important since this diversity originates from locally adapted populations which may be more vulnerable to pressures such as climate change. If lost this reduces the overall diversity and fitness of the species (Lyam *et al.*, 2022).

Many attempts have been made, dating from the early 1900s, to determine the number of biomes and classify their ranges (Mucina, 2019). A recent study from Keith *et al.* (2020), in conjunction with the International Union for Conservation of Nature (IUCN), recognises six major terrestrial biomes: tropical-subtropical forest, temperate-boreal forests, shrublands and shrubby woodlands, savannahs and grasslands, deserts and semi-deserts, and polar-alpine. These can then be further divided into 29 subtypes (Keith, 2020). Other studies have applied wider or finer gradation in the classification of biomes, but for our purposes here, we will describe patterns of genetic diversity within the three major forest biomes outlined by the IUCN. Using these more wide-ranging definitions permits us to present the way in which genetic diversity generally manifests in these biomes while still leaving space for nuance.

5.4.2. Short summary of major forest biomes and within species genetic diversity trends

The International Union for Conservation of Nature (IUCN) outlines three major forest biomes: tropical-subtropical forests, temperate-boreal forests, and shrublands/shrubby woodlands. All three exhibit certain similarities, with the most obvious being the prevalence of trees and woody vegetation

(Keith, 2020). Another defining characteristic is the presence of high levels of biodiversity: forests account for over 80% of all terrestrial animal species. They are pivotal to the health of the wider planet, acting as habitats, biodiversity centres, and carbon sinks, so successfully conserving them is vital (Aerts and Honnay, 2011). As mentioned earlier, differences in forest biomes are largely a result of climate and precipitation, giving rise to differing seasonalities, characteristics, and typical tree species.

Tropical-subtropical forests biome (e.g., South America, Central Africa, and Southeast Asia)

Tropical and subtropical forests occur around the equator and beneath the tropics. Tropical forests circumscribe the globe, stretching across the equatorial regions of South America, Africa, and Southeast Asia. This transitions into subtropical forest below and above 23.5° of latitude, though the tropic front is pushed further north in Southeast Asia due to mountains and coastal winds which prevents winter frost and increases moisture (Ashton and Zhu, 2020, Percy and Robichaux, 1985). Several sub types of these forests exist.

Purely tropical rainforest occurs in lowlands close to the equator and is effectively aseasonal: temperature and precipitation remains high and relatively constant year-round, and the landscape is densely populated by a thick canopy of evergreen broadleaf trees (Percy and Robichaux, 1985). Deciduous trees are sometimes present depending on soil fertility. Subtropical rainforests, which occur closer to the tropic edges, for instance in southern China or Brazil (Chi *et al.*, 2017, Keith *et al.*, 2022) exhibit similar characteristics to tropical ones, but have a semi-evergreen character with a higher proportion of deciduous or partly deciduous species. In addition, precipitation is seasonal and changes throughout the year (Percy and Robichaux, 1985). Productivity is extremely high in rainforests, maintained by the temperature and moisture, and accordingly this supports the highest levels of biodiversity on the planet.

In contrast to rainforest, tropical and subtropical dry forest have less annual rainfall and a pronounced seasonality distinguished by a longer dry season. This is driven by increased distance from the equator and coast, and they are found in inland areas in southern Latin America and Asia, and parts of Southern Brazil and Central America. Trees are smaller in stature and consists of a higher proportion of deciduous species (Murphy and Lugo, 1986).

Tropical and subtropical montane forests occupy a set of regions throughout the tropics, populating uplands and the foothills of mountains. Temperatures are comparatively colder than wet and dry tropical forests while rainfall is kept fairly constant due to cloud cover from the increased altitude (Bruijnzeel and Veneklaas, 1998). Altitude also drives speciation and dictates the structure and composition of the forest (Salinas *et al.*, 2021).

Case study: diversity and life history in the Neotropics

The Neotropics consist of South America and the tropical regions of Central America, though for the purposes of this case study we will consider only the tropical and subtropical regions of this realm. Genetic structure is generally impacted as expected by the parameters discussed earlier, with the exception of seed dispersal mechanism.

Genetic differentiation within species tends to be high across tropical forests, something corroborated in the Neotropics (Table 5.2). There are several causes. Species are often present at low population density levels and in smaller ranges, while pollination is mainly insect or animal mediated known to have a shorter range of dispersion than wind (Loveless, 1992; Thang *et al.*, 2020). When carried out abiotically, gravity is the main mechanism, as the effectiveness and range of wind is much reduced due to the density of tropical and subtropical forest (Degen and Sebbenn, 2021). These all restrict dispersal and therefore gene flow over large areas. Highly asynchronous rainfall patterns over short distances may also be a driving factor as they can dictate flowering patterns, forming potential barriers to gene flow (Gamba and Muchhala, 2020). Pioneer species have also been noted to have higher genetic differentiation and lower diversity than later successional stage trees due to founder

effects (when a population has reduced genetic diversity due to being descended from a small number of colonisers) (Lowe *et al.*, 2018).

While these life history traits may be expected to lead to lower genetic diversity and higher inbreeding when compared to temperate-boreal forests, research has shown this is not the case, with similar levels of genetic diversity found for trees across both biomes (Loveless, 1992). Tropical trees use various methods to maintain this. Outcrossing is widespread and highly preferential among species, though rates vary across taxa (Ward *et al.*, 2005). Many have self-incompatibility mechanisms, such as the growth of only male or female flowers on individual trees. Both increase the likelihood of mating with a genetically distinct individual. Inbreeding is also strongly negatively selected for (Degen and Sebbenn, 2021). There is also evidence that the pollen dispersal mechanisms of neotropical trees have greater range than expected, with many carrying pollen hundreds or thousands of metres. This helps to maintain gene flow and supports outcrossing for populations (Ward *et al.*, 2005). As a result of this, tropical and subtropical tree species often present with genetically differentiated subpopulations which are themselves genetically diverse (Lowe *et al.*, 2018).

The genetic resilience of tropical tree species is especially vulnerable to accelerating anthropogenic habitat fragmentation and devastation. These disrupt corridors for gene flow and upset the often-delicate relationships relied upon for pollination, depriving tropical species of the ability to maintain high genetic variability and therefore fitness (Vinson *et al.*, 2018). Studies have already shown that outcrossing is reduced in logged and fragmented populations, predicted to reduce genetic fitness and diversity (Ward *et al.*, 2005).

Table 5.2 Genetic diversity and governing processes in tropical-subtropical forest. Summary of the impact of life history and population characteristics typical of tropical-subtropical tree species on genetic diversity.

PROCESS	KEY TRENDS	IMPACT
Range size	Low	<ul style="list-style-type: none"> - Increased population differentiation - Reduces gene flow and genetic diversity
Population density	Low	<ul style="list-style-type: none"> - Increased population differentiation - Reduced gene flow and genetic diversity
Pollination mechanism	Predominantly animal or invertebrate	<ul style="list-style-type: none"> - Increased population differentiation - Reduced genetic diversity - Reduced gene flow (though may be more efficient than previously thought)
Mating system	Predominantly outcrossing	<ul style="list-style-type: none"> - Maintains higher genetic diversity - Reduced inbreeding
Refugia present	May be present in Amazon	-

Temperate-boreal forests and woodlands biome (e.g., North America, Europe, and East Asia)

Temperate-boreal forests and woodlands are widely distributed across the Northern Hemisphere, covering large portions of North America, Europe, and the Asiatic part of the Russian Federation, as well as sections of East Asia. Additionally, smaller temperate-boreal biomes exist in Patagonia, southern Australia, and New Zealand (Willis, 2009). The transition from temperate to boreal forest, also called taiga, occurs with increasing latitude, driven by lower temperatures and rainfall. It stretches across the cold regions of the northern Russian Federation, Scandinavia and Canada, encircling the Arctic. Each forest subtype is dominated by different classes of plant: deciduous broadleaf trees are prevalent in temperate forests (especially in the Northern Hemisphere) while conifers account for the majority tree species in the taiga (Apps *et al.*, 1993).

Marked seasonality is a significant feature of temperate forests, driven by large temperature changes between the winter and summer months. This variability regulates growth and breeding and divides the forests annual life cycle into two phases. The first occurs in summer months, accompanied by active tree growth. In winter they effectively enter hibernation, facilitated by a range of adaptations and processes: the inhibition of growth, storage of sugars, increased ‘hardiness’, and, most well-known, the dropping of leaves (Willis, 2009).

In contrast to temperate woodlands, boreal forests experience colder temperatures, often below freezing for much of the year, and are subject to shorter growing seasons (Gauthier *et al.*, 2015). As conifers dominate here forests are largely evergreen, particularly at northerly latitudes, and so lack the leaf shedding characteristic of temperate forests (Neale and Wheeler, 2019). It should be noted that there is not a sharp separation between forest subtypes: a transitional zone exists with a patchwork of deciduous and coniferous trees, often occupying better and poorer quality soil respectively. Secondary factors such as this also promote diversity across the biomes, giving rise to localised populations and species’ differentiation (Esseen *et al.*, 1997).

Case study: diversity and life history in temperate biomes (Europe and North America)

Both boreal and temperate forests exhibit high genetic diversity, while population differentiation is lower when compared to tropical forest (Table 5.3). This is facilitated by large population sizes and ranges along with the dominance of wind pollination, ensuring steady gene flow (Gamba and Muchhala, 2020). Differences are also found between the two, with temperate forest and species showing the highest genetic differentiation and boreal the lowest (Aguinagalde *et al.*, 2005; Karnosky *et al.*, 1991). This is likely influenced by the favouring of outcrossing and preponderance of wind pollination among conifers. The higher levels of ploidy seen in angiosperms (the predominant tree form in temperate biomes) is likely also a factor, as it causes genetic differences between populations due to chromosome number changes. (De La Torre *et al.*, 2017).

The establishment of genetic refugia during glaciation in the last ice age, followed by their expansion after its end, is a unique feature of Northern Hemisphere temperate-boreal biomes and has influenced their modern-day genetic landscape. A common pattern is seen where populations of higher genetic diversity are clustered around areas corresponding to past refugia, while diversity decreases with distance from these. This is due to founder effects from individuals re-colonising land previously under ice and radiating out with a smaller fraction of species total diversity (Tzedakis *et al.*, 2013). Species with higher number of glacial refugia, which were of a larger range and more continuous, have also been shown to have increased diversity today (Roberts and Hamann, 2015).

Table 5.3 Genetic diversity and governing processes in temperate-boreal forest. Summary of the impact of life history and population characteristics typical of temperate-boreal tree species on genetic diversity.

PROCESS	KEY TRENDS	IMPACT

Range size	High	<ul style="list-style-type: none"> - Lowered population differentiation - Increased gene flow and genetic diversity
Population density	High	<ul style="list-style-type: none"> - Lowered population differentiation - Increased gene flow and genetic diversity
Pollination mechanism	<p>Wind for gymnosperms,</p> <p>Mixed for angiosperms</p>	<ul style="list-style-type: none"> - Lowered population differentiation, increases gene flow and maintains high genetic diversity in conifers - Comparatively higher genetic structure and slightly lower genetic diversity in angiosperms
Mating system	<p>Outcrossing for gymnosperms</p> <p>Mixed for angiosperms</p>	<ul style="list-style-type: none"> - Lowers population differentiation, increases gene flow and maintains high genetic diversity in conifers - Comparatively higher population differentiation and slightly lower genetic diversity in angiosperms
Refugia present	Widespread	<ul style="list-style-type: none"> - Hotspots of genetic diversity surrounded by radiating populations of lower diversity

Shrublands and shrubby woodlands biome (e.g., Australia)

Shrublands and shrubby woodlands are variously known as scrub, bush, or chaparral, among other terms. There is more uncertainty as to what constitutes shrubland, due both to the diversity of climate zones shrublands inhabit and overlap with other biomes such as grasslands, deserts, and montane (Woodward *et al.*, 2004). However, there are agreed characteristics of this biome. It is populated largely by shrubs, smaller woody vegetation which usually reaches to a maximum of 2 metres, and small trees (Woodward *et al.*, 2004). Cover tends to be sparser than forests, with a reduced canopy and wider spacing between vegetation between which other plants grow. These aspects are a result of the lower precipitation and soil fertility usually apparent in shrublands, as it limits the growth of taller trees (Eastman *et al.*, 2013; Keith, 2020).

Limiting, sometimes extreme, conditions are the defining factor of shrublands, varying by location. Temperate and Mediterranean zones are subject to large differences between summer and winter temperatures while subtropical and desert shrublands suffer from high daily temperatures. All are subject to aridity, low precipitation, and drought (Rutherford *et al.*, 2006). Recurrent disturbances, most notably fire, shape the composition of shrublands by removing biomass and promoting stand replacement (Paysen *et al.*, 2000; Pausas and Bond, 2020).

Due to the varying climates shrubland occurs in it does not form large, continuous biomes, a trait known as azonal (i.e., not dictated by climate), leading to a fragmented distribution throughout the biosphere. Shrublands are therefore found in arid sections of Australia, Africa, and Central America,

around mountainous regions in South American and Central Asia, and near steppe and grassland across all continents except Antarctica (Keith, 2020).

Case study: diversity and life history in Australia (mixed biomes inc. tropical-subtropical, shrubby woodland)

Australia presents something of a unique case. The country is home to a wide variety of biomes, ranging from tropical forest in the north to shrubland and temperate forest in the south, with the centre covered by a large arid zone (Keith, 2020). Additionally, Australian plant species have a fairly independent evolutionary history to the rest of the world. Nevertheless, they still follow the general trends dictated by life history traits outlined earlier in section 5.3, with those exhibiting higher abundance, range, and continuity displaying higher levels of genetic diversity (Table 5.4).

The Australian tropical biome is present in the north and north-west of the country, consisting mainly of seasonal forest. While previously widespread, aseasonal tropical rainforest has been steadily reduced in Australia for 20 million years and is now only present in isolated pockets (refugia) along the north-east coast (Pennington *et al.*, 2004). Lower genetic diversity in the seasonal forest which constitutes the vast majority of Australia's tropical biome is seen in comparison to the western and eastern portions of the country and may reflect the decreasing range and population of the tropical biome over time (Broadhurst *et al.*, 2017). That genetic differentiation is also higher in this biome than in other tropical and subtropical provides further evidence for this as it could be a function of shrinking, more isolated populations, and genetic drift.

The eastern and western portions of the country consist of two distinct biomes, a temperate and Mediterranean and temperate climate respectively, which both transition into shrubland towards the arid centre. Genetic diversity has been shown to be highest in the temperate biome, likely a result of several factors (Broadhurst *et al.*, 2017). While aridification pushed all three biomes towards the continent edges this was less pronounced in the temperate region. In addition, a more varied topography allowed certain species to escape this by moving south or upwards in altitude, which preserved genetic diversity (Byrne *et al.*, 2008). Trees also make up the majority of plant species here in comparison to the Mediterranean biome where there is a greater proportion of shrubs, which have been shown to have less genetic diversity than Australian trees. This is unusual: as woody taxa, both have been found to exhibit similar levels of diversity in other biomes, and the discrepancy here may be a result of a more localised distribution and smaller ranges for Australian shrubs.

A final point to note is the higher differentiation present in Australian trees compared to those in other continents. This leads to more localised and genetically distinct populations and is likely driven by two factors. The first of these is the greater fraction of insect and wind pollinated trees in Australia which have a reduced range of pollen dispersion, especially compared to majority wind pollinated temperate-boreal forests (Gamba and Muchhala, 2020). The second of these is habitat fragmentation, which is assumed to be more widespread in Australia than elsewhere (Broadhurst *et al.*, 2017). This should be especially noteworthy for conservation: genetic studies can be used to properly direct efforts such as seed banking, while this fragmentation means Australian tree species may be more susceptible to habitat destruction caused by human activities.

Table 5.4 Genetic diversity and governing in processes in tropical-subtropical forest. Summary of the impact of life history and population characteristics typical of tropical-subtropical tree species on genetic diversity.

PROCESS	KEY TRENDS	IMPACT

Range size	Small	<ul style="list-style-type: none"> - Increases population differentiation - Reduces gene flow and genetic diversity
Population density	Low (tropics and shrubland) High (temperate forest)	<ul style="list-style-type: none"> - Increases population differentiation - Reduces gene flow and genetic diversity - Reduced population differentiation - Increased gene flow and genetic diversity
Pollination mechanism	Mixed	<ul style="list-style-type: none"> - Insect or animal pollinated species expected to have lower diversity and gene flow and higher genetic structure than wind pollinated species
Mating system	Mixed, outcrossing not as widespread as trees but still widespread	<ul style="list-style-type: none"> - Helps to maintain gene flow and genetic diversity when outcrossing
Refugia present	In tropical biome	<ul style="list-style-type: none"> - Contracting, show reduced diversity

5.5. Conclusions

Predicting the level and distribution of genetic diversity within forest trees is complex since the forces which shape it can interact and intersect. For example, Rossetto *et al.* (2020) demonstrated that genetic structure and diversity can even differ across the same landscape among multiple species within the *Acacia* genus. The authors suggested that “informative replicated patterns are likely to emerge from largescale, standardized, multispecies comparisons”. With some nuances, we now can do this for trees and woody plant species, drawing from the growing body of empirical research. Indeed, of their ecological and life history traits are linked to general trends of higher levels of genetic diversity, lower genetic differentiation, and lower levels of inbreeding when compared to other plants (such as herbaceous annuals). These include (Cavers and Cottrell, 2015; Petit and Hamp, 2006; Hamrick and Godt, 1996, Hamrick *et al.*, 1992):

- Greater population range and size;
- Far-reaching pollination/seed dispersal mechanisms such as wind or animal ingestion;
- Tendency to favour outcrossing;
- Long-lived with overlapping generations.

Nevertheless, there are numerous external forces which can reduce the genetic diversity of tree species. Many of these are a direct result of human action and behaviour. Habitat clearance can fragment populations and reduce diversity, especially in animal or insect pollinated trees (Ward *et al.*,

2005), while climate change will affect tree species in myriad ways, changing ecological and selective pressures and potentially breaking up population ranges (Lyam *et al.*, 2022). Carefully managing the impact of how all these factors influence genetic diversity will be essential if we wish to conserve it.

5.6. References

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PART 3: STATE OF FOREST GENETIC RESOURCES CONSERVATION

CHAPTER 6. *IN SITU* CONSERVATION OF FOREST GENETIC RESOURCES

6.1. Introduction

Forest resources continue to be threatened globally by a multifold of pressures, including anthropogenic land use change, fragmentation, habitat destruction, indiscriminate forest burning, overharvest, mining, climate change, pollution, inappropriate silvicultural practices, and the use of forest reproductive material poorly adapted to local conditions (Liebhold *et al.*, 2017; Seidl *et al.*, 2017; McDowell *et al.*, 2020; Guo *et al.*, 2022). These drivers of degradation may not necessarily lead to a loss of species but rather of populations, causing genetic erosion, which implies a loss of alleles, modifying their frequencies in a given place within populations or across species (Quiñones-Pérez *et al.*, 2017). This in turn may cause a reduced capacity of species to cope with ongoing stresses and future threats (Bijlsma and Loeschke, 2012).

In situ conservation is specifically targeting individual populations of species in their natural environment, where they have developed their distinctive characteristics (Frankel *et al.*, 1977; FAO, 2014). The *in situ* approach to conserve forest genetic resources presents several advantages over *ex situ* conservation as it aims to maintain evolutionary processes and adaptation to environmental changes. It does not exclude using the conserved resources, maintains ecological, aesthetic, ethical and cultural values of tree species, and allows to conserve multiple species at the same time. In addition, costs per unit of genetic diversity are lower than for *ex situ* conservation efforts, which may not be a viable option for many tree species (Gapare, 2013), mainly due to the recalcitrant nature of their seed or due to the large space needed and high costs implied in the set up and maintenance of seed orchards.

This *in situ* conservation approach is often implemented in protected areas where naturally regenerating wild populations are found. However, the approach can also be applied in managed production forests (e.g. timber concessions) and multiple-use forests (e.g. community-managed forests) (FAO, DFSC and IPGRI, 2001). Considering that protected areas are becoming increasingly isolated by habitat fragmentation (Hannah *et al.*, 2007), for many species significant portions of their gene pools are found outside the boundaries of protected areas. For example, a recent study showed that, for 63 socioeconomically important tree species in Southeast Asia, 74% of the most important areas for *in situ* conservation of populations were outside protected areas, whereas all species were found to be severely threatened across nearly 50% of their native ranges (Gaisberger *et al.*, 2021). Very similar results were reported by Ceccarelli *et al.* (2022) for socio-ecologically important priority tree species in Central Africa, and by Fremout *et al.* (2020) in the dry forests of southern Ecuador and northern Peru. Thus, it is clear that conservation in protected areas needs be complemented by conservation efforts in other forested areas, communal lands, forest patches within agricultural landscapes, naturally regenerating production forests (i.e. where management is directed towards maintaining natural regeneration), and by setting aside representative forest areas for genetic conservation. Similarly, other tree-based systems (e.g. agroforestry) should also be targeted by conservation efforts (Chirwa *et al.*, 2008; Dawson *et al.*, 2013).

While the importance of genetic diversity metrics for biodiversity conservation has become widely recognized, research has mainly focused on species with an economic value or iconic status (e.g. Wehenkel *et al.*, 2017) and major gaps remain particularly for a large number of threatened tree species (e.g., imperiled oaks in the United States of America, Backs *et al.*, 2021). In the absence of genetic characterization data, it is often necessary to use proxies, such as demographic indicators and ecological or environmental factors, to develop genetic conservation plans..

Another limitation is that the findings from research on tree species' genetic diversity have not yet been systematically incorporated into conservation planning and decision making (Hoban *et al.*, 2013; Torres-Florez *et al.*, 2019), even in regions where genetic studies relevant for the conservation and management of tree species have been most extensive (e.g. Pérez-Espona *et al.*, 2017). There are also other knowledge gaps. For example, the well-known red-listing system developed by IUCN for classifying the threat status of species has serious limitations in quantifying threats at population level

(Ceccarelli *et al.*, 2022) and currently it does not include intra-specific diversity. Thus, it does not consider potential adaptive processes of species to future environmental change (Rivers *et al.*, 2014).

Nevertheless, research on genetic diversity has grown more quickly in vascular plants as compared to other groups of organisms (e.g., mammals, arthropods and fish), at least in Europe (Torres-Florez *et al.*, 2019). A number of local, national and regional assessments on the conservation of forest genetic resources have been conducted in the last decade (e.g. Proschowsky *et al.* (2020) for five Nordic countries; Wang *et al.* (2020) for native tree species in British Columbia, Canada; Backs *et al.* (2021) for native oaks in the United States of America; Climent *et al.* (2021) for Mediterranean pines). Similar efforts need to be urgently carried out in lower income countries where the vast majority of forest genetic resources are located.

In the definition of conservation priorities, growing emphasis has increasingly being placed on the floristic dimension of biodiversity, while in the past, conservation typically privileged areas with presence of large fauna. Research made during the last decade has brought along more efficient approximation of taxonomic boundaries (particularly in Africa; see for example Daïnou *et al.*, 2017; Ahossou *et al.*, 2020; Ewédjè *et al.*, 2020) and improved understanding of natural histories of tree species. In addition, growing evidence is pointing towards large spatial convergence between the distribution of intraspecific diversity and interspecific diversity for plant species, as revealed by research conducted in the African continent (see Vellend and Geber *et al.*, 2005 for theoretical background and Duminil *et al.*, 2013; Dauby *et al.*, 2014; Sosef *et al.*, 2017; Demenou *et al.*, 2020 for findings related to African tree species). Similarly, in the Mediterranean region, research combining species occurrence, phylogenetic diversity and functional trait diversity have revealed clear hotspots of intraspecific diversity where to focus conservation efforts of specific tree populations (Albassatneh *et al.*, 2021; Fady *et al.*, 2022).

Range-wide assessments of genetic diversity and international research collaborations are important means to inform and guide effective *in situ* conservation of forest genetic resources in the face of various challenges, particularly the pressure posed on forest resources by land use changes, habitat destruction, environmental changes and with pests and diseases.

6.2. Systematic approach for conserving forest genetic resources

A dynamic approach to *in situ* conservation of forest genetic resources facilitates evolutionary processes, such as natural selection and adaptation to environmental changes, fits best to trees as long-lived organisms and is thus the most efficient option for conserving the gene pools of tree species (Kelleher, 2018). *Ex situ* conservation (see Chapter 7) in seed banks and field collections complements *in situ* conservation.

In situ conservation facilitates natural regeneration and selection, and contributes to safeguarding tree species against biotic and abiotic threats (Graudal *et al.*, 2014; Kelleher 2018). This approach is ideally implemented through networks of sites distributed across ecological zones, in a way that it comprehensively represents different forest ecosystems and the diversity found within them. This effectively maintains viability and integrity of targeted populations, species and communities, and considers a diversity of ecological, economic and social objectives (Potter *et al.*, 2017).

The principles guiding *in situ* conservation of forest genetic resources, developed in the 1980s (e.g. Ledig, 1986), are still generally valid. The selection of stands and populations for inclusion in a network of gene conservation areas for a particular species should be based on the distribution of genetic variation. The minimum size of conservation stands identified as priorities can be highly variable depending on the conservation goal (e.g., targeting low-frequency genes; Yanchuk 2000). Generally, the size of the area to be conserved relates to the density of reproducing trees of the target species to ensure minimum effective population sizes (Frankham *et al.* 2014a), so this can vary largely from a few to hundreds of hectares (FAO *et al.*, 2001).

Globally, genetic information and knowledge to fine-tune conservation efforts and strategies are still lacking for most tree species. Methods are divided based on whether conservation priorities are established based on genetic information, or this is not available. In the first case, priorities can be

defined by assessing the contribution of specific populations to the total neutral genetic diversity of a target species (Petit *et al.*, 1998). In the second instance, ecological and geographical information are used as proxies for genetic variation (e.g., Hamann *et al.* 2005; Koskela *et al.* 2013). These genecological approaches have been commonly adopted in the past (Graudal *et al.* 1997), under the assumption that the distribution of genetic variation parallels patterns of ecological variation. In herbaceous plants and shrubs collected over the European Alps, freely available environmental and geographic distance variables were found to be highly effective surrogates in conservation planning for representing adaptive and neutral intraspecific genetic variation (Hanson *et al.*, 2017). With regard to forest genetic resources, ecological zones were used to identify gaps in conservation efforts in British Columbia (Canada), using variation in macroclimates as a proxy for adaptive genetic variation (Hamann *et al.*, 2005; Wang *et al.*, 2020).

A similar approach has been used to develop a pan-European network of genetic conservation units (de Vries *et al.*, 2015) using a climatic stratification of Europe (Metzger *et al.*, 2013) to identify a minimum set of conservation units distributed across different climatic zones and countries, representative of the broad range of genetic variability found across the target tree species. Investigations have been conducted on the relationships between species attributes and genetic parameters in Australian plant species, with the objective to improve predictions of genetic parameters from these relations, drawing on species population theory and previous global analyses (Broadhurst *et al.*, 2017).

With regard to proxies for genetic diversity, plant demography, genetics and sexual and asexual reproduction in plants are inter-related processes, each shaping the others. In particular, the reproductive system of a tree species has substantial impact on its genetic diversity and structure within and among natural populations. The many modes of sexual reproduction in angiosperms reflect the combinations of floral traits, existence of self-incompatibility mechanisms and interactions with pollinators. Species' dispersal and life history traits also affect genetic structure. The body of research on these themes, in support of conservation action, has grown to cover a greater number of species (e.g., Dompreh *et al.*, 2015; Ewédjè *et al.*, 2015; Duminił *et al.*, 2016).

Life history traits and range size were found to be key correlates of genetic diversity in a study focused on neotropical tree species (Lowe *et al.*, 2018), which revealed some general patterns. For example, pioneer and narrow range species showed lower levels in genetic diversity but a greater variance, revealing signs of founder effects and more pronounced genetic drift (see also Chapter 5). In addition, species dispersed by animals compared to other dispersal strategies showed lower population differentiation, possibly an indication of extensive gene flow. Finally, species dispersed by abiotic agents and pioneer species presented a more pronounced fine-scale genetic structure, indicating the occurrence of restricted seed dispersal and family cohort establishment (Lowe *et al.*, 2018). On the other hand, recent evidence is suggesting that the most widespread and ecologically variable Amazonian tree species may counter the effects of genetic erosion through admixture between related species, a mechanism by which species of long-lived plants may acquire novel alleles (Larson *et al.*, 2021).

6.2.1 Range-wide spatial analyses guiding conservation

Two key questions in conservation are what to conserve and for which purpose. Successful *in situ* conservation programmes require a clear definition of objectives, including the maintenance of evolutionary processes, a balanced use of resources and long-term access to forest resources to enable sustainable use (Kelleher 2018). In the past, priorities have centered around maintaining stands or individual trees with superior traits, in light of their use for breeding. Nowadays conservation efforts are targeting also specific natural populations for their insurance value. Their identification is based on the assessment of genetic variation, which has a defined spatial structure, resulting from interactions among a complex suite of factors.

Ideally, conservation planning should consider the entire standing genetic variation of the species targeted for conservation (Crandall *et al.*, 2000). The identification of populations to be safeguarded is

guided by spatial analyses. Range-wide studies on genetic diversity of tree species have grown significantly in the last decade and targeted a significant number of tropical and subtropical tree species. These studies are based on molecular markers and assist in the identification of populations that host high or low levels of genetic variation, and of lineages potentially having unique traits critical for adaptation, due to a differential natural selection (Marchelli *et al.*, 2017; Potter *et al.*, 2017). A growing number of tree species have been characterized for their spatial genetic structure and diversity across a diversity of geographic and ecological contexts. Such examples include tree species in seasonal dry forests of South America (Melo *et al.*, 2014; Thomas *et al.*, 2016; Bocanegra-González *et al.*, 2018; Bocanegra-González *et al.*, 2019; Adriana *et al.*, 2020; Aguirre-Morales *et al.*, 2020), temperate tree species (Awad *et al.*, 2014; Tsumura *et al.*, 2014; Chiocchini *et al.*, 2016; Ruhsam *et al.*, 2016; Aradhya *et al.*, 2017; Hu *et al.*, 2017; Kwak *et al.*, 2017; Schoettle and Coop, 2017; Mapelli *et al.*, 2018; Stojnić *et al.*, 2019; Belton *et al.*, 2021; Kavaliauskas *et al.*, 2021; Nocchi *et al.*, 2022), species in Central America (Alcalá *et al.*, 2014; Hansen *et al.*, 2014; Larranaga *et al.*, 2017; Flores *et al.*, 2019) and in the Amazonian region (Sujii *et al.*, 2015; Rollo *et al.*, 2020) and as well as in Sub-Saharan Africa (Gwali *et al.*, 2014; Addisalem *et al.*, 2016; Pakull *et al.*, 2019; Bouka *et al.*, 2022) and in South-East Asia (Hartvig *et al.*, 2018; Saini *et al.*, 2018; Hartvig *et al.*, 2020; Hirata *et al.*, 2021).

A growing number of studies has also focused on rare, endemic, threatened tree species with small and isolated populations (e.g. Tamaki *et al.*, 2016; Quiñones-Pérez *et al.*, 2017), and these investigations are very insightful, given that species with small and isolated populations tend to be more exposed to the impacts of genetic drift and inbreeding (Jaramillo-Correa *et al.*, 2009). In Mexico, where the highest diversity of pine and oak species worldwide is found, a recent review of forest genetic resources conservation efforts revealed a very poor characterization of tree genetic diversity and biased towards Pinaceae (Jaramillo-Correa *et al.*, 2017). This suggests a need for harmonizing the markers used to enable comparability of estimates among the studied species and to unveil general regional trends across species.

Phylogeographic research has expanded considerably, through a diversified range of studies on tree species past refugia and spatial distribution of main gene pools, with examples from temperate tree species (Cubry *et al.*, 2015; Dering *et al.*, 2017; Gömöry *et al.*, 2018), in the Mediterranean region (Piotti *et al.*, 2017; Sękiewicz *et al.*, 2018; Walas *et al.*, 2019; Viruel *et al.*, 2019; Cheikh Albassatneh and Escudero, 2021), Sub-Saharan Africa (Lompo *et al.*, 2018; Monthe *et al.*, 2018; Monthe *et al.*, 2019; Donkpegan *et al.*, 2020; Rimlinger *et al.*, 2020), Latin America (Thomas *et al.*, 2015), North America (Zinck *et al.*, 2016), and South-East Asia (Chen *et al.*, 2019). The findings of these studies have significant implications for improving conservation in the face of climate change, as well as examining the role that refugia can help to protect constituent species and ecosystems over long spans of time. Morelli *et al.* (2020) provided an overview of the different climate-change refugia that can be found along a set of spatial and temporal ranges, including disturbance refugia that maintain ecosystems in a state of constant perturbation, preventing over a long time their transitions into other types of systems. They also propose to translate climate-change refugia conservation into action, by implementing spatially explicit efforts that consider site-specific conditions and connectivity.

Conservation priorities can be identified based on threat assessments and supported by habitat suitability models (also known as species distribution models or ecological niche models). These are very useful tools to map the potential distribution of species' whose range may not be fully known, to examine the spatial distribution of a target species across different ecological regions, and to spatially track the potential impact of threats, particularly of future climate changes. Spatial threat analyses have been extended to a growing number of tree species, including crop wild relatives. Ceccarelli *et al.* (2022) examined the distribution of 100 socio-ecologically important priority tree species in Central Africa and the spatial extent of main threats to these species.

6.2.2 Effective population size

An important aspect in conserving evolutionary resilience of individual tree populations is to maintain a large enough size to host sufficient genetic variation and consequently enable evolutionary

processes to continue. Effective population size (N_e) is a critical parameter in population genetics, determined based on molecular markers, with important practical applications in conservation genetics as it defines the rate of genetic drift and loss of genetic variability in a population; yet its estimation presents major challenges. Some authors reviewed and compared existing methods to estimate N_e from genetic data to assess their performance; they found considerable variance (Kimberly *et al.*, 2015; Wang *et al.*, 2016) and identified methods that are more versatile under different scenarios (Waples *et al.*, 2016).

In the 1980s, some authors (Franklin, 1980; Soulé, 1980) proposed $N_e = 50$ as sufficient to prevent inbreeding depression in naturally outbreeding diploid species in the short term, and $N_e = 500$ to avoid genetic drift. According to Frankham *et al.* (2014a; 2014b), evidence had grown to review these recommendations upward, and they suggested that this size of $N_e = 50$ is inadequate to prevent inbreeding depression over five generations in the wild, and rather $N_e \geq 100$ would be necessary. In addition, even $N_e = 500$ is indicated by the same authors as too low to retain evolutionary potential for fitness in perpetuity and better results would be achieved with $N_e \geq 1000$. Franklin *et al.* (2014) replied to the critical comments still recommending the 50/500 as a useful guide. Another critical parameter is the estimate of a Minimum Viable Population size (MVP), used to establish recovery targets for endangered species, strongly supported by some conservation scientists promoting the use of generic rules based on known MVPs values published in the literature, to guide assessment and recovery of data deficient species (Reed *et al.*, 2003; Traill *et al.*, 2007).

Rosenfeld (2014) suggested that Population Viability Analysis (PVA) and the 50/500 rule is still valid against theoretical background and are complementary, as they represent both short- and long-term recovery targets in endangered species planning. More recently, the debate resumed during the development of the Kunming-Montreal Framework for Biodiversity, which includes the goal of maintaining genetic diversity. Laikre *et al.* (2020) recommended that the framework should refer explicitly to maintaining genetic diversity within all species and also defined indicators of progress toward this goal, based on information about the number of species, populations, or metapopulations whose size is sufficient to maintain genetic diversity, the number of species or populations monitored with regard to their intraspecific diversity, and based on measured loss of populations with distinct traits in target species. Hoban *et al.* (2020) further stressed the need to include targets and indicators for genetic diversity in the framework, and to apply them to all species. These authors also proposed a pragmatic set of indicators: number of populations with effective population > 500 , proportion of populations conserved for target species, number of species and populations in which genetic diversity is assessed over time via DNA-based methods. They underlined that only few countries, in their reporting to the CBD, refer to genetic monitoring using DNA data or to aspects related genetic diversity, and generally the reports do not refer to intraspecific variation in forest resources (Hoban *et al.*, 2021a).

While Hoban *et al.* (2021b) underlined that $N_e > 500$ was a suitable threshold, other authors (Fady and Bozzano, 2021) highlighted the difficulties in deriving N_e values in natural populations and the fact that in forest trees contemporary gene flow is abundant. Therefore, defining the boundaries of a population could be very challenging, especially for species with a low density and patchy distribution. In addition to these difficulties, the lack of genetic data for some species would prevent countries from setting priorities for their conservation. Considering these aspects, the regional network in Europe (EUFORGEN) proposed modification to an existing indicator used by European countries to track genetic conservation efforts and species' range-wide trends in conservation at regional level. The revised indicator is composed of four sub-indicators (Lefèvre *et al.*, 2020) and does not include N_e , while it considered counting the number 1) of populations effectively conserved (conservation effort), 2) of species conserved compared to species growing in the country (species diversity index), 3) of ecological zones targeted compared to ecological zones found in the country (ecozone diversity index) and 4) of ecological zones containing more than one population effectively conserved (insurance index). Santos-del-Blanco *et al.* (2022) remarked that estimating contemporary N_e in forest tree populations is particularly difficult for monitoring large continuous tree populations or small gene conservation units positioned within large continuous tree populations; they suggested

that the use of other approaches based on monitoring demography, mating system and reproductive success may be more feasible to assess temporal changes in N_e . However, accurate demographic predictions would be equally challenging and would require large investments in fieldwork for data collection.

It is important to note that while Hoban *et al.* (2021b) recommended targeting wild populations for conservation of at least 500 individuals, referring to all organisms, target population sizes vary considerably among taxa and thresholds in population sizes for inclusion in conservation areas should be determined based on species-specific biological traits (Minter *et al.*, 2021). For forest trees, in most cases, while 500 or more reproducing trees would be ideal to conserve genetic diversity of widely occurring and stand-forming conifers or broadleaf species), 50 reproducing trees should be sufficient to conserve adaptive or other traits in marginal or scattered tree populations (Koskela *et al.*, 2013).

6.2.3 *The role of protected areas, managed forests and trees on farms*

In situ conservation of forest genetic resources is frequently carried out outside protected areas, on land managed based on a diversity of arrangements regarding ownership and use. A recent study based on a database including over 46 000 tree species assessed their range protection and anthropogenic pressures to develop conservation priorities (Guo *et al.*, 2022). It showed that a large proportion of tree species receive limited protection by the existing protected areas, and that a large portion of their range is under great human pressure (Guo *et al.*, 2022). A spatially explicit regional assessment of main threats (overexploitation, fire, overgrazing, habitat conversion, and climate change) affecting forest ecosystems, focusing on socio-economically important tree species in Asia, showed that about two-thirds of the most important areas for their conservation were located outside protected areas (Gaisberger *et al.*, 2022a). The study also identified some natural areas across Borneo rain forests as important hotspots for *in situ* conservation of forest genetic resources, and these priority sites are also largely (82%) outside protected areas. Another study, based on a similar methodological approach and focusing on 16 important food tree species in Burkina Faso, revealed a very limited coverage of protected areas where the targeted species co-occur and threats are most severe (Gaisberger *et al.*, 2017). In Asia, a study targeting three highly valuable rosewood species (*Dalbergia cochinchinensis*, *D. cultrata* and *D. oliveri*) and assessing their vulnerability to key threats indicated that the species investigated appear to be highly threatened also in areas covered by protected areas (Gaisberger *et al.*, 2022b).

Utilization of forest resources does not necessarily compromise conservation efforts. The management of forest species outside of strict *in situ* reserves (sometimes called *circa situ* or near site conservation) should be based on the principles of landscape ecology and adaptive management. A study conducted in North America showed that old-growth and second-growth populations of Eastern white pine (*Pinus strobus*) presented similar levels of genetic diversity in genes considered related to adaptive responses to climate in tree species (Rajora *et al.*, 2021). The findings suggested also that these results could be potentially extended to most conifer tree species in boreal and temperate forest ecosystems.

6.2.4 *Setting targets and priorities*

Research on intraspecific diversity can focus on two elements: a) neutral genetic diversity, which provides insight on population dynamics and evolutionary forces (genetic drift, mutation and migration) and b) adaptive genetic diversity, which reflects the way organisms manage to adapt to new environmental conditions. Most conservation studies have so far focused on neutral markers to determine the genetic variation and population structure, and to define conservation priorities, even though variation in these markers may correlate poorly with traits under selection and does not necessarily reflect the evolutionary potential of a species.

Adaptive genetic diversity should be primarily targeted by conservation, due to its relevance in the long run, but this has been generally neglected in conservation planning, given the difficulties in

measuring it directly. Nowadays, advanced genotyping techniques, combined with improved statistical methods, are providing the tools by which adaptive genetic diversity can be more easily estimated, facilitating large-scale analyses. Teixeira *et al.* (2021) suggested that, to develop effective genetic conservation strategies, understanding functional genetic diversity, demographic history, and ecological relationships would be necessary rather than assessing neutral genetic diversity. On the other side, DeWoody *et al.* (2021) presented arguments in favor of assessing neutral genetic diversity, as this is closely tied to evolutionary fitness. Other authors have suggested that not only genetic variation is of interest but also gene flow and selection play a key role in determining whether a population can effectively adapt or not to environmental changes (e.g. Aravanopoulos, 2016).

Fernandez-Fournier *et al.* (2021) tested if standing genetic variation could be used as proxy for adaptive genetic variation on lodgepole pines (*Pinus contorta*) in western Canada. They found that their priority populations for conservation identified based on adaptive variation alone were not significantly divergent from priorities defined through genome-wide genetic variation. They concluded that a simple analysis of mean genome-wide genetic variation would enable to identify local adaptation and set priorities accordingly. Based on these authors, adaptive diversity is only a small proportion of the genome or consist of many loci with small effect. In addition, under conditions in which fragmentation and bottlenecks occur and drift overwhelms selection, both neutral and adaptive diversity would be similarly affected.

Priority populations can also be identified based on a combination of genetic parameters. Ottenwell *et al.* (2016) proposed using a scoring defined by important parameters, such as population differentiation, genetic diversity and inbreeding, measured for the plant population of conservation concern, in relation with representative ‘healthy’ populations used as a reference. Other authors suggested to account for both key neutral and adaptive components of genetic diversity in a complementary way (Funk *et al.*, 2012; Rodriguez-Quilon *et al.* 2016) for the identification of conservation units below the species level, particularly in tree species showing a marked population structure and complex evolutionary histories. Given their higher resolution, genomic data can be particularly useful to delineate conservation units especially for rare, endangered species, for which the detection of adaptive genetic variation is difficult (Funk *et al.*, 2012).

In the past, discussions have also revolved around whether to focus conservation of locally common versus low-frequency alleles. Locally common alleles were thought to indicate the presence of genotypes adapted to specific environmental conditions (Frankel *et al.*, 1995). In the view of some, rare alleles appear mainly as unfavorable mutations, as evolutionary relics, which provide little contribution to the overall fitness of a species (e.g. Brown 1989). Other authors (e.g. Gapare *et al.* 2005; 2013) suggested that rare alleles can be very important for long-term evolution, also in relation to resistance to pathogens. It has also been debated if conservation priority should be placed on peripheral or central parts of the distribution range of a species (Lessica and Allendorf, 1995) with populations found at the edge of the species distribution expected to present lower genetic diversity and higher genetic differentiation those located in the central part of the range (Pandey and Rajora, 2012). Currently, new approaches, such as ecological genomics, allow to define more precisely conservation priorities, by generating better estimates of adaptive genetic potential for tree species at different scales (Eckert *et al.* 2013; Pais *et al.* 2017; Liu *et al.* 2016) (*see section 6.3*).

Challenges arise in circumstances where conservation actions are focused on species found in very fragmented landscapes heavily modified by human interventions, where species are affected by some degree of isolation, or when conservation is targeting species that occur at low densities, have small population sizes, and are rare or peripheral. Understanding patterns of genetic diversity at the landscape scale of fragmented or remaining populations is of great importance in the development of conservation action plans, especially when these populations are found in peripheral portions of a species range. Marginal populations are potentially more exposed than core populations to risks of extinction related to natural or anthropogenic pressures (e.g., lags in adaptation) and most likely host unique diversity in terms of evolutionary potential, particularly interesting in the context of climate change (Fady *et al.*, 2016; Piotti *et al.*, 2017; de Dato *et al.*, 2020; Csilléry *et al.*, 2020). Peripheral

and marginal populations have received increasing attention in recent years, being considered as “natural laboratories”, where complex interaction take place involving demographic processes and natural selection, providing examples of whether adaptation can keep the pace with environmental changes (Fady *et al.*, 2016; Ducci *et al.*, 2017; Curtu *et al.*, 2017, Huber *et al.*, 2017; Kelleher *et al.*, 2017; Rusanen *et al.*, 2017), particularly those changes affecting the rear edge of the distribution range. These portions of the range pose the greatest conservation challenges and can be used to experiment adaptive forest management approaches aiming at both conservation and sustainable management purposes (Fady *et al.*, 2016).

Investigating a narrow endemic island tree species, *Cedrus brevifolia*, occurring in just one population, Eliades *et al.*, (2019) concluded that maintenance of genetic diversity should be regarded as one of the main prerequisites for the long-term survival of the species and suggested to have in place several small conservation units where to adopt dynamic *in situ* conservation efforts and at the same time derive material to establish *ex situ* efforts. In Canada, a large number of species are at the northern edge of their distribution and may be at risk. Research focused on populations of *Magnolia acuminata* found that although the species has a fragmented habitat, peripheral populations presented high levels of genetic diversity (Budd *et al.*, 2015). Nevertheless, levels of gene flow appeared relatively low, possibly leading to progressive isolation, posing questions on the long-term survival of the species in Canada. Limited pollen dispersal, despite being a wind pollinated species, and low connectivity were found also in *Quercus robur* in refugial populations at the species’ southern range margin (Moracho *et al.*, 2016). Different landscape features of oaks' refugial habitats were considered responsible for what observed (e.g., rugged topography combined with dense vegetation and humid microclimate), together with occurrence of local mating, possibly favoured by high tree compatibility. Genomic insights enabled to increase understanding of the evolutionary history and population structure of another tree species, *Cupressus gigantea*, a rare conifer from the eastern Qinghai–Tibet Plateau, located in extreme environments above 3 000 metres above sea level and allowed to cast light on its potential to adapt to climatic changes (Yang *et al.*, 2022).

A large number of small populations are at increased risk of extinction because genetics and evolutionary biology are not sufficiently considered in conservation planning. A science-based approach has been proposed by some authors to systematically address cases where management of fragmented populations would be necessary for their conservation, evaluating opportunities to restore gene flow to small inbred populations, when the risk of outbreeding depression is low (Ralls *et al.*, 2017). More generally, habitat fragmentation and disturbance activities (e.g., logging) are expected to produce significant genetic consequences, such as reduced genetic diversity, increased genetic differentiation and potentially increased inbreeding. However, research has shown that forest tree species are able to cope with these pressures through a range of responses (e.g., increased gene flow via pollen and/or seed, overlapping generations occurring in a single site delaying the loss of genetic diversity, flexible mating systems), which vary largely across species and are very nuanced (Lowe *et al.*, 2015). In order to understand the major consequences of forest fragmentation, attention has been pointed away from adult populations towards a focus on progeny in impacted landscapes and its relative success in regenerating, on the mating and breeding systems, on the specific landscape context and nature of the disturbance (Lowe *et al.*, 2015). Species-specific mechanisms are at play in ensuring persistence, despite occurrence in very fragmented and specialized habitats, such as in the case of *Eucalyptus caesia*, whose survival seems to be related to the ability to resprout and expand from a lignotuber despite small population size and minimal genetic interconnection with other individuals (Bezemer *et al.*, 2019).

Alteration of habitat by a combination of human activities and climate change affects most of the alpine timberline area. Results from research conducted on Swiss stone pine (*Pinus cembra* L.) in the Carpathians and the Alps (Dzialuk *et al.*, 2014) suggested that the effects of changing climatic conditions on the genetic structure of this species may take place with significant delay, due to its long-life span. A growing number of studies in different geographic areas is being conducted on tree species occurring at different densities and with varying mating systems, to characterize their responses to fragmentation and to different types of disturbance (e.g. *Olea europaea* subsp. *cuspidata*

in Afromontane highlands of Ethiopia (Kassa *et al.*, 2017), *Vateria indica*, a Dipterocarpacea, and *Dysoxylum malabaricum*, a large canopy tree, both found in the Western Ghats, South India (Ismail *et al.*, 2014a, 2014b), and *Parkia biglobosa*, a legume tree of great value from the parklands from West Africa (Lompo *et al.*, 2020)).

In some extreme circumstances, *in situ* conservation may not be sufficient to secure the survival of relic populations and knowledge about the spatial scale and heterogeneity of intra-specific distribution of genetic diversity is necessary to inform *ex situ* conservation efforts, as in the case of the IUCN red-listed Serbian spruce (*Picea omorika*) found in some refugial populations in the Balkans. For this species, Aleksić *et al.* (2017) carried out a whole population genetic characterization and found a highly complex fine-scale spatial genetic structure, over a small area of just 0.34 hectares.

6.2.5 Conservation in relation to pest and diseases management

Early genetic studies have focused primarily on traits of economic importance such as growth and wood quality rather than pest resistance, although forest health issues are becoming more pressing every day due to the effects of non-native insects and diseases and the expansion of native pathogens favoured by climate change (Holliday *et al.*, 2020). Management of pest and diseases is often neglected among the goals of conservation, but maintaining diversity at intraspecific level produces positive outcomes in the fight to mitigate the impacts of pathogens. Conserving diversity keeps levels of overall population fitness high and enhances the chances of finding individuals and populations with resistance to specific pathogens. Herbivory by insects is more contained in diverse forests and mixed versus monospecific stands, especially when phylogenetic distance among tree species is greater (Jactel *et al.*, 2021). This generates a ‘dilution’ effect on host species, and a consequent reduction of growth and spread of pathogens, particularly when these are not generalist species (Keesing *et al.*, 2010). There is also an indirect effect of diversity on increased resistance to pathogens due to the reduced level of drought-related stress experienced by high-diversity stands (Rasche *et al.*, 2013). However, recent research conducted across a very large dataset of more than 130 000 forest plots in the United States of America has shown that two contrasting effects are simultaneously at play, facilitation of pest diversity and dilution, and their interaction and relative strength depend on the overall diversity of native tree species (Guo *et al.*, 2019). When this diversity is high, the effects of non-native pathogens are contained (Guo *et al.*, 2019).

Research findings have shown that many forest tree species present some degree of genetic resistance, even if very limited, to most pathogens or insects (Woodcock *et al.*, 2017). Screening intraspecific diversity in natural stands to explore its relationship with variation in resistance to pest and diseases is a strategy that has been adopted for some tree species for a few decades, but today this is conducted with the support of advanced genomic tools, which can improve the way forest health problems are addressed (National Academies of Sciences, Engineering, and Medicine, 2019). New tree genomic resources available have contributed to the understanding of the genomic architecture of insect and disease resistance, and to the development of both conventional breeding and genetic engineering (Naidoo *et al.*, 2019).

The ash dieback in Europe, caused by the fungus *Hymenoscyphus fraxineus*, has had a major impact on the survival of European ash (*Fraxinus excelsior*) populations across its range (Baral *et al.*, 2014; Enderle, 2019). Phenotypic and genotypic selection have been used to identify putatively resistant ash individuals, showing that genotypic selection is a faster approach than phenotypic selection (Chaudhary *et al.*, 2020) and that trees disease resistance and tolerance traits appear to be under the control of many genes with small effect (Sollars *et al.*, 2017). The polygenic nature of complex traits conferring resistance may limit the power of marker-supported selection. Nevertheless, genome-wide association studies can work in cases when disease resistance traits have simpler genomic architecture, like in the case of American beech (*Fagus grandifolia* Ehrh.), an ecologically important species growing in eastern North America, for which a major gene for beech bark disease resistance was identified (Čalić *et al.*, 2017). A tree species that is currently posing significant concerns is *Dalbergia sissoo* Roxb., an important nitrogen fixing leguminous multipurpose tree originating in an area from the southern parts of the Islamic Republic of Iran to India but planted worldwide. In the last

two decades the species has been under pressure by over exploitation and various pathogens, mainly fungi causing root rot and vascular wilt diseases (Shah *et al.*, 2021), and some initial screenings to identify resistant genotypes have been conducted (Harsh *et al.*, 2011, Dobhal *et al.*, 2019).

There is a question whether traditional *in situ* conservation efforts are enough to safeguard forest genetic resources against future challenges. Genomic biosurveillance has been proposed as a new solution based on DNA signatures, which help to accurately identify pests and pathogens, attribute detected samples to specific sources of pathogens, to identify pathways that facilitate spread, predict invasiveness and pathogenicity of organisms (Bilodeau *et al.*, 2018; Hamelin and Roe, 2020). Having such a system in place would slow invasions. Ferrenberg *et al.* (2016) reminded the influences of landscape features on pest dynamics and on forest pest-host interactions, which are bound to become progressively more difficult to predict under rapidly changing environmental conditions.

6.3 Scientific advances supporting *in situ* conservation

6.3.1 New approaches for vulnerability assessments and priority-setting

Threat assessments and vulnerability analyses of tree species are part of the priority setting process and are critical for conservation planning. The main threats to tree populations are habitat destruction, land use changes, exploitation and climate change (Kelleher, 2018). These pressures determine the impact on forests and their genetic diversity, cause habitat fragmentation, and may disrupt gene flow at landscape level. A series of spatial threat assessments have been conducted covering multiple threats over both individual and multiple species.

Van Zonneveld *et al.* (2018) looked at threats at intraspecific level on 80 socioeconomically viable tree species in South America under eight scenarios by 2050, using a spatially explicit method based on Ecogeographic Range Segments (ERSs), which are groups of populations of a certain species in a specific ecological zone of a particular grid cell of a species' geographic occupancy. The results pointed clearly to the need to set up a regional action plan for the conservation of forest genetic resources in South America and identified the species most at risk (*Balfourondendron riedelianum*, *Cariniana legalis*, *Dalbergia nigra*, *Handroanthus pulcherrimus*, *Pachira quintana*, *Prosopis flexuosa*, and *Prosopis pallida*).

With the aim to set priorities in conservation planning, another multi-species study examined the increasing demographic and climatic pressures, which are threatening indigenous trees in Burkina Faso (Gaisberger *et al.*, 2017). The study focused on 16 species that contribute substantially to income generation and nutrition in rural households in agroforestry parklands. In this study, a species-specific and spatially explicit approach was developed combining freely accessible datasets, species distribution models (SDMs), climate models and expert survey results to predict, at fine scale, where six key threats to them (overexploitation, overgrazing, fire, cotton production, mining and climate change) were likely to have the greatest impact. Different interventions were recommended based on the predicted level of threat for all species, both individually and collectively. The concept can be applied anywhere appropriate spatial data and knowledge of local experts are available.

Another investigation focused on understanding the vulnerability to anthropogenic threats of the 50 most common tree species of the tropical dry forests of northwestern Peru and southern Ecuador to assist restoration and conservation efforts (Fremout *et al.*, 2020). The effects of future climate change and four current threats (fire, habitat conversion, overgrazing and overexploitation) on these target species were assessed using an ensemble modelling approach to predict species distribution ranges. This employed freely accessible spatial datasets to map threat exposures. In addition, a trait-based scoring approach to estimate species-specific sensitivities was developed, using differentiated trait weights in accordance with their expected importance in determining species sensitivity to specific threats. The results suggest that current levels of habitat conversion, overexploitation and overgrazing pose threats to most of the studied species larger than climate change. A spatially explicit planning strategy for species-specific restoration and conservation actions was also derived from the assessment.

A different method based on multicriteria risk mapping and on a multi-attribute frontier concept was used by Yemshanov *et al.* (2013). Their conservation assessment was based on the concept that locally adapted populations of wide-ranging species may lag behind their optimal climate conditions under climate change. The assessment led to the identification of which populations within the distributions of a tree species would be most in need of genetic conservation actions, as most likely to experience adaptational lags in coming decades, based on bioclimatic envelope models.

The USDA Forest Service has coordinated tree species conservation assessments specific to the United States of America or to regions of the country, through the CAPTURE project, targeting 419 forest tree species across 48 contiguous States and Alaska (Potter *et al.*, 2017). The project used a data- and expert- opinion-driven hierarchical framework that categorizes species into vulnerability classes and relate them to associated strategies for maintaining adaptive genetic variation through monitoring, management, and conservation (Potter *et al.*, 2017). Conceptually, species are categorized based on the three dimensions of vulnerability: threat exposure, threat sensitivity, and adaptive capacity relative to the threat (Foden *et al.* 2013). Priority setting has also been carried out for the wild relatives of tree species that are important food, forage, medicinal, ornamental or industrial crops. This effort involved different experts (forest geneticists, ecologists, silviculturists, entomologists, and pathologists) in the species-specific assessment of the vulnerability of the targeted tree species to climate change, to insect and disease threats, and associated severities. High-risk species were then identified together with areas where these were most in need of conservation activity and monitoring.

A complete threat assessment was performed evaluating the short-term threats from overexploitation, overgrazing, landslides, and fragmentation as well as long-term threats from climate change for common walnut (*Juglans regia* L.) wild and cultivated populations across three Central Asian countries (Kyrgyzstan, Tajikistan and Uzbekistan), showing high threat levels in the walnut selected populations, particularly due to overgrazing and overexploitation (Gaisberger *et al.*, 2020). The research enabled also to identify sites suitable for *in situ* conservation based on level of threats and genetic diversity.

Contrasting effects of human impact on genetic diversity were detected in two West African timber tree species with differing successional status, a pioneer (*Triplochiton scleroxylon*) versus non-pioneer species (*Mansonia altissima*) (Akinagbe *et al.*, 2019). The study suggested that non pioneer tree species could be more prone to genetic erosion than pioneer tree species as a result of adverse human impacts. Therefore, conservation of genetic diversity in both pioneer and non-pioneer tree species populations would likely necessitate different measures. A spatially explicit framework was applied to assess the vulnerability of three highly valuable Asian rosewood species (*Dalbergia cochinchinensis*, *D. cultrata*, *D. oliveri*) to five key threats across their native range in six countries of the Greater Mekong Subregion. Species-specific priority areas for conservation and restoration were identified and subdivided by ecoregions as a surrogate for delineating adaptive variation within species (Gaisberger *et al.*, 2022). The study set the basis for regional planning for other valuable tree species.

6.3.2 Application of genetic, genomic and biotechnological tools

Genomic approaches appear increasingly more promising in assisting conservation practice (Segelbacher *et al.*, 2022). Genome-wide data provide novel insights and can contribute to improve traditional conservation genetic inferences (Shafer *et al.*, 2015; Plomion *et al.*, 2016; Neale and Wheeler, 2019). A significant progress in the last 10 years has consisted in the ability to use genomic data to look at the extent of local adaptation, in individuals and populations (also of rare, endangered species; Funk *et al.*, 2012), which can be detected even over very short spatial scales (Neale and Wheeler, 2019). While earlier attempts to explore local adaptation were based mainly on targeting candidate genes, or on finding neutral markers linked to adaptive loci, nowadays screening the whole genome holds much more power to unveil mechanisms that lead to evolutionary change, such as polygenic and epistatic selection (Plomion *et al.*, 2016). New technologies span across different

domains from genetics, molecular biology, bioinformatics, to robotics applied to study structure, function, and evolution of genes, by means of high-throughput methods. Higher quality information has been generated on past population history of tree species, species boundaries have been more efficiently delimited, inference of phylogenetic relationships between species has improved, and molecular level characterizations of adaptive evolution in forest trees have been carried out (Dauby *et al.* 2014; Heuertz *et al.* 2014; Plomion *et al.*, 2016; Neophytou *et al.*, 2022).

Approaches based on transcriptomic, proteomic and metabolomic data have been adopted to investigate highly complex traits (e.g., Depardieu *et al.*, 2021). These methods, in combination with genome-wide variation data, enable to explore causal linkages between genotype and phenotype, through statistical modeling (Marjoram *et al.* 2014; Benestan *et al.*, 2016). It must be noted that despite all these advances, the interpretation of genomic data is challenging and risks to remain within the research domain, without having an effective influence on practice in the field (Shafer *et al.*, 2014).

With regard to the application of genomic data to address selection of tree populations to be conserved, few practical examples are available for forest trees. In *Pinus sylvestris*, genomic data from a relatively small number of adaptive genes have confirmed the high level of differentiation and unusual evolutionary history of populations from Scotland (Wachowiak *et al.* 2011). In *Populus trichocarpa*, an extensive genome scan revealed geographic differentiation patterns at different scales in western North America (Slavov *et al.* 2012). Use of genomic data also assisted in clarifying issues related to taxonomic complexity, unrecognized clonality and hybridization, as in the case of two rare species of eucalyptus, *Eucalyptus virginea* and the putative hybrid *E. × phylacis*, in need of conservation (Bradbury *et al.*, 2021). Genomic data are also advancing insights on inbreeding depression occurring in natural populations (Kardos *et al.*, 2016).

Landscape-level approaches have also grown and show potential to address conservation and management questions (Keller *et al.*, 2014). The regional landscape has an influence on local populations, but a critical question is about the spatial scale of this effect, and how this differs based on the type of response measured. Jackson and Fahrig (2014) showed the importance of managing large buffers around sites targeted for conservation; managing protected species at spatial scales that are based on population abundance may lead to neglect broader landscape effects on population genetic diversity and persistence. The identification of the spatial co-occurrence of landscape features and significant genetic discontinuities between populations reveals the spatial distribution of diversity and the divergence of populations (Chiocchini *et al.*, 2014; Mattioni *et al.*, 2017), with implications in selecting priority sites for conservation. Ecological genomics is an interdisciplinary field that seeks to understand responses of organisms to their natural environment by applying functional genomics to identify and characterize genes with ecological and evolutionary relevance (Ungerer *et al.*, 2008; Renn *et al.* 2010; Holliday *et al.*, 2016; Lu *et al.*, 2019). Landscape genomics is another rapidly advancing multidisciplinary research field that combines population genomics, landscape ecology, and spatial analysis to assess the influence of environmental heterogeneity on neutral and adaptive genetic variation (Hand *et al.* 2015; Balkenhol *et al.*, 2017).

In relation to the landscape scale, a number of studies have been conducted on geneflow through pollen, linking this knowledge to its applications in conservation (Ellstrand *et al.*, 2014; Gerber *et al.*, 2014; Millar *et al.*, 2014; Williams *et al.*, 2017). Research on pine pollen has revealed its aerodynamic properties and revealed the importance of vertically uplifted pollen, which participates in meso-scale transport and interacts with atmospheric processes, partly maintaining its capacity to germinate and fertilize seed moving long distance through meso-scale transport (William *et al.*, 2017). These findings have strong implications with regard to the potential effects of forest fragmentation and the design and management of genetic conservation units. A revived interest in geneflow and its capacity to counteract mutation, drift, and selection, even at low intensity, is supported by new data-rich genomic techniques which enable to examine more closely its role in plant evolution and how it varies according to the species, the specific populations investigated, and within the same population over time (Ellstrand *et al.*, 2014).

Finally, new biotechnological tools have been developed to mitigate the effects of pathogens on forest tree species. An example is provided by American chestnut (*Castanea dentata*), a formerly dominant or co-dominant tree, which has been made functionally extinct by an invasive fungal pathogen. After several decades of research to find a solution, blight-tolerant American chestnut individuals were developed through genetic engineering, introducing a gene from wheat producing an enzyme that enables the tree to break down the oxalate produced by the pathogen (Steiner *et al.*, 2017; Powell *et al.*, 2019).

6.4 Implications of climate change and other threats for *in situ* conservation

Impacts of climate change on forests include potential changes in species ranges, species composition, vulnerability to pests and diseases, potential adaptation or changes in performance (Alfaro *et al.*, 2014; Kelleher *et al.*, 2015). In the face of climate change, the *in situ* conservation of forest genetic resources may need to be actively supported by management measures, including silvicultural treatments, monitoring of vitality of the populations conserved and natural regeneration, the selection of units for conservation that contain altitudinal and other ecological gradients, the adoption of assisted migration to establish tree populations better adapted to expected future climatic conditions (Kelleher *et al.*, 2015). To fully understand the consequences of global climatic changes on biodiversity, in the last decade, a significant amount of research has focused on assessing how climate change is expected to impact the current *in situ* conservation efforts, assessing climate change exposure, vulnerability, sensitivity and adaptive capacity of individual tree species (Bower *et al.*, 2017a; Lima *et al.*, 2017; Serra-Varela *et al.*, 2017), and defining ways to incorporate climate change considerations into *in situ* conservation strategies.

Modelling the impact of climatic changes has been extended to wild relative of fruit trees, identifying 150 global sites, located mainly but not exclusively inside protected areas, which would be suitable for *in situ* conservation (Vincent *et al.*, 2019). Knowledge about the past history of tree species, the expansions and contraction of their distribution ranges in the face of climate change has grown in the last 10 years particularly for regions of the world that are less known, such as Sub-Saharan Africa (Budde *et al.*, 2013; Hardy *et al.*, 2013; Heuertz *et al.*, 2014; Duminial *et al.*, 2015; Piñeiro *et al.*, 2017; Lompo *et al.*, 2018; Migliore *et al.*, 2019; Migliore *et al.*, 2020; Ahossou *et al.*, 2020; Donkpegan *et al.*, 2020; Helmstetter *et al.*, 2020; Piñeiro *et al.*, 2021; Vanden Abeele *et al.*, 2021; Lyam *et al.*, 2022).

Knowledge of local adaptation informs conservation goals. Plant species can tolerate changing climatic conditions or avoid them through habitat shifts; these reactions depend on the levels of adaptive capacity or ecological plasticity. Some analytical approaches to determined species' vulnerability have been based on a series of parameters (e.g., life history traits, distribution, and pest and pathogen data, combined with consensus regional climate; Bower *et al.*, 2017) while others have been developed using habitat suitability models and spatially explicit future predictions of species' ranges (e.g. Chakraborty *et al.*, 2021). Spatial models showing the potential impacts of climate change have been improved by including consideration of the fact that species may extent their distribution beyond their present realized niche, and the physiological limits that shape their distribution may also change under the selective pressure posed by climate change itself. Scoble and Lowe (2010) have suggested to incorporate neutral and non-neutral genetic diversity in the form of phylogeographic and landscape genetic data into species distribution modelling approaches, to improve climate-related conservation planning. Catullo *et al.* (2015) developed a general framework to include impacts key parameters associated with physiological limits and adaptive evolution into spatial models of climate change. Benito Garzón *et al.*, (2019) used an emerging modelling approach, DTraitSDM, to be able to link current species distribution ranges with phenotypic plasticity and species traits associated with local adaptation of fitness, measured across large geographical gradients. Rare and threatened tree species are considered more vulnerable to climate change and quantitative genetics experiments across multiple environments, to understand a species' ability to withstand future environmental changes, have been highly valuable to measure phenotypic plasticity, its heritability and the way

evolution acts on favourable traits and simultaneously on others that may limit adaptation (Edwards *et al.*, 2015).

Alberto *et al.* (2013) reviewed the knowledge gained from 250 years of common garden experiments and were able to observe that most forest trees have evolved local adaptation. They recorded particular problems at the range margins and highlighted the need for more targeted modeling addressing specific issues affecting populations at the southern and northern margins. Ramírez-Valiente *et al.* (2022) conducted a similar assessment on Mediterranean forest species. Hoban *et al.* (2016) reported about the limitations of genomic tools in detecting the underlying genetic basis of local adaptation, and Flanagan *et al.* (2018) argued that, in some circumstances, common garden experiments are more efficient to derive information on local adaptation than studies based on genomic tools in investigating adaptive variation. These authors provided recommendations on how to design experiments, analyze data and collaborate with genomics experts, to assist monitoring programmes and conservation. A study conducted on seedling of lodgepole pine (*Pinus contorta*) in common garden trials with populations from across western Canada demonstrated that genomic data are very useful when used in combination with phenotypic data but can also work as substitutes for phenotypic data to guide management of tree populations in the face of climate change, when phenotypic trials cannot be established (Mahony *et al.*, 2019).

Evidence has fully emerged that, in multiple organisms including trees, most complex traits are polygenic, and are characterized by a genetic architecture determined by numerous loci, all showing a small effect (Rajora *et al.*, 2016; Miguel *et al.*, 2022). A study conducted on fitness-related traits in maritime pine (*Pinus pinaster*) also suggested that polygenic adaptation can occur rapidly, and this has implications regarding the capacity of natural forest tree populations to adapt to future environmental changes, whose projections should be re-examined in light of these findings.

Evolutionary theory provides answers to conservation management questions (Eizaguirre and Baltazar-Soare 2014). “Adaptive introgression” is the process through which new variations are incorporated in a population via geneflow, from either the same species or a different species, and are maintained by natural selection, conferring an increased fitness (Burgarella *et al.*, 2019). Adaptive introgression can contribute to mitigating the consequences of limited adaptive potential associated with standing genetic variation and mutation, and could enable a relatively fast response to changing environmental conditions (Hamilton and Miller, 2016; Suarez-Gonzalez *et al.*, 2018). Advances in genomic tools have contributed to better understanding this phenomenon, to detect signatures of selection in introgression, to link adaptive introgression to phenotypic variation and fitness through improved statistical techniques (Suarez-Gonzalez *et al.*, 2018). These refined approaches allow to prioritize conservation units maximizing evolutionary potential (Eizaguirre and Baltazar-Soare 2014). Natural hybrid zones in forest trees have been targeted by research as model systems to analyse the transfer of adaptive genetic variation by introgression (Suarez-Gonzalez *et al.*, 2016; Menon *et al.*, 2021).

Research-based decision-making approaches have been proposed to support conservation planning in light of climate changes, whose impacts may not be adequately handled by conventional conservation approaches. Shoo *et al.* (2013) provided recommendations on a range of actions that span from *in situ* conservation in existing species refugia to various degrees of mobility enhancement of populations and *ex situ* conservation outside the natural environment. They also invited to pay attention to aspects such as the likelihood of obtaining positive results from interventions, the relationship between costs and benefits, and the benefits that generate positive effects also on non-target species.

The framework designed by Bower *et al.* (2017b) to identify priority populations for gene conservation is based on maps of risk of extirpation in the face of climate change, overlaid with maps showing the spatial distribution of genetic variation across a species range. Highest conservation priority (in the form of establishment of *ex situ* collections) is assigned to populations exposed to immediate threats, such as fire, disease, insects, invasive species, and human development. The second highest priority is attributed to populations expected to be outside of the future climatic niche

of the species based on the best available models, followed by those populations which are currently found within the future climatic niche of the species, but are at exposed to potential maladaptation to the new climatic conditions. Aspects such as potential for migration are also considered. Particular attention is reserved to species with disjunct populations and populations at the trailing edge of climate change.

Gray *et al.* (2017) proposed a novel approach to identify current and potential future within-species conservation gaps across the range of 54 forest tree species in western North America. Current species distribution models were examined in relation to the location of protected areas and the expected velocity of climate change. Interior and boreal tree species were found to be potentially most vulnerable, although currently best protected *in situ*. Conservation efforts prioritized across multiple jurisdictions were recommended.

Christmas *et al.* (2016) reviewed the types of constraints that plants may face to adapt (e.g. lack of available space for migration, excessively fast rate of environmental change, lack of connectivity in the landscape, compromised niche availability, poor dispersal ability, low level of plasticity, etc.). They assessed available methods to screen the adaptive potential in tree species, including observations along natural environmental gradients and analyses of genome and transcriptome. Based on this, they identified conservation approaches most appropriate for different circumstances. These mainly consisted in conservation *in situ* targeting genetic refugia and remnant populations, the creation of biodiversity corridors, assisted migration and geneflow, and translocation to novel suitable habitats. Concerns about risks outweighing benefits in introducing foreign genetic variation to face challenging environmental conditions have been raised (Aitken and Whitlock, 2013; Whiteley *et al.*, 2015). Nevertheless, new DNA sequencing technologies can be used to detect local adaptation and identify “preadapted” genetic variants from source populations within the species range that can be moved into recipient populations to increase their evolutionary potential and capacity to withstand drastic environmental changes. This strategy seems to be more beneficial for trees, compared to other organisms, given their long life and limitations in dispersal (Aitken and Bemmels, 2016; Gugger *et al.*, 2017).

A range of studies have been conducted to elaborate genetic resource conservation strategies in the face of climate change for a diversity of tree species and locations, including the Cerrado biome (Diniz-Filho *et al.*, 2018), where the proposed strategies to set priority were different between regions with predicted stable and unstable environmental conditions; for endemic North American redwoods (Ahuja *et al.*, 2017); for Patagonian *Nothofagus* forests (Marchelli *et al.*, 2017), where current hotspots of genetic diversity seem to coincide with convergence zones of different expansion routes of the species investigated, most likely resulting from admixture; for different European countries (Skørppa and Fjellstad, 2017; Postolache *et al.*, 2019; Šijačić-Nikolić *et al.*, 2019) and for the pan-European region, where the vulnerability of dynamic genetic conservation units of forest trees has been assessed (Schueler *et al.*, 2013) and the establishment of additional genetic conservation units, specifically to respond to climate change, has been recommended (Kelleher *et al.*, 2015).

Genetic diversity and evolutionary processes support species continuous adaptation to evolving conditions across multiple scales, from fine scale to landscape and ecoregions (Fady *et al.*, 2020), through both natural processes as well as assisted adaptation and active management, aided by improved knowledge on genomic diversity and evolutionary mechanisms. For those species that occur in small, isolated populations and are experiencing a decline in fitness and evolutionary potential, genetic rescue has been proposed as a strategy to complement *in situ* conservation efforts, when these may not be sufficient. To predict a possible future of tree populations, particularly in the face of climate change, and to determine which conservation strategies would be most appropriate (*in situ* or *ex situ*), the genomic offset approach has been proposed. This is based on genomic and environmental data used to predict the optimal genetic composition for a targeted tree population that would enable it to adapt to the modeled future environmental conditions, determining the degree of potential maladaptation, defined as the ‘distance between the current and required genomic composition in a set of putatively adaptive loci’ (Rellstab *et al.*, 2021). The approach has been applied in very few cases so

far and requires proper testing. Other authors (Arenas *et al.*, 2021) have proposed the use of genomic prediction (GP) models to study the evolution of relict natural populations and consequently design conservation measures. The approach, normally used in crop breeding to predict occurrence of traits of interest and shorten the length of the breeding cycle, was piloted to predict the performance of introduced saplings of sacred fir (*Abies religiosa*) in a managed population of this species in Mexico. The preliminary results obtained indicated that further efforts should be directed towards this approach, suitable particularly for small and isolated natural populations of endangered non-model species.

Genetic rescue aims at increasing (neutral) genetic diversity of a population through the movement of individuals between populations (Whiteley *et al.*, 2015). Potential disadvantages are outbreeding depression, resulting from mixing genotypes with divergent adaptation, or the disruption of co-adapted gene complexes. A combination of advanced genomic tools, which can characterize adaptive differences among populations, and neutral markers, which provide answers regarding the amount of gene flow between populations, can be used to reduce the risks of outbreeding depression (Weeks *et al.*, 2011). Nevertheless, this approach has had limited application (Whiteley *et al.*, 2015) and encountered also cultural barriers (Love Stowell *et al.*, 2017), despite evidence of positive outcomes in most cases where it has been adopted, for invertebrates, vertebrates and plants (Frankham, 2015). Translocation has also been attempted for rare and endangered tree species (Ren *et al.*, 2020).

6.5 Socioeconomic aspects of *in situ* conservation

The loss of genetic diversity has been portrayed as a hidden crisis with large repercussions for human society as intraspecific variation supports ecosystem functions and provides material, non-material, and regulating contributions to people (Des Roches, 2021). A survey on attitudes towards forestry and nature protection conducted in 2017 in Serbia showed that in the opinion of stakeholders, the most supported methods for the conservation of forest genetic resources was the designation of seed stands and conservation in protected areas (Šijačić-Nikolić *et al.*, 2017). In addition, most respondents thought it was necessary to intensify action to promote conservation of forest genetic resources. Another study conducted in Spain showed that society is willing to pay for research programs on forest genetic resources, particularly focusing on improving resistance to biotic risks (Solíño *et al.*, 2020). The study also revealed that research on transgenic forest resources is not socially accepted.

Evidence is emerging about effective technical and governance approaches to conserving forest ecosystems and their genetic resources developed by local communities. To determine the value of traditional management systems in the conservation of *Araucaria angustifolia* in southern Brazil, Zechini *et al.* (2018) compared genetic diversity in this species in populations traditionally managed and populations located within protected areas, without finding significant differences, demonstrating that traditionally managed land use systems can be equally effective and would help maintain culturally sound practices. Thomas *et al.* (2017) validated traditional and crowdsourced knowledge on seed production of Brazil nut trees in the Peruvian Amazon and Fremout *et al.* (2021) incorporated local ecological knowledge to guide tree species selection in tropical dry forest restoration. Furthermore, Stoian *et al.* (2019) produced evidence of how forest concessions in the Multiple Use Zone (MUZ) of the Maya Biosphere Reserve (MBR) in Petén, Guatemala, generated socioeconomic benefits for local communities and at the same time contributed to the conservation of the areas under concession, where high value species (e.g., mahogany) were well maintained and deforestation levels were close to zero. A meta-analysis of published case-studies compared land use and land cover change data in protected versus community managed forests. The results showed that community managed forests had lower and less variable annual deforestation rates than protected forests (Porter-Bolland *et al.*, 2012), highlighting the potential value of local institutional arrangements and locally driven governance in supporting tropical forest conservation.

With regard to equitable sharing of benefits, a study carried out in Guatemala demonstrated the practical functioning of the Nagoya Protocol, applied to a case where local communities granted permission to scientists to conduct a non-commercial study on gene flow in populations of a highly

valuable timber species, *Swietenia macrophylla* King, in the Maya Biosphere Reserve of Petèn (van Zonneveld *et al.*, 2018). The case turned out to be an exemplary experience of participatory research that generated a common understanding between users, providers, and potential beneficiaries of genetic resources and contributed to create a positive attitude towards the use of molecular genetics to carry out conservation of genetic diversity of tropical species.

Groups and individuals differentiated based on social attributes, such as gender, wealth, age, ethnicity, have a different perception of the value of forests, different access and use rights and motivation to conserve natural resources. Research on social aspects and forest genetic resources has focused on further characterizing gender-differentiated knowledge, preferences and priorities of diverse social groups, reflected in the identification of priority species and their management and including species and traits for conservation, domestication, utilization (Carney and Elias 2013; Elias 2015, 2017; Karambiri *et al.* 2017; Rimlinger *et al.*, 2021a,b; Gachuri *et al.*, 2022). This work has contributed to support the idea of a legitimate involvement of both women and men in natural resource management. Focusing on shea- nut tree (*Vitellaria paradoxa*) management and selection in Burkina Faso, Carney and Elias (2013) showed how the knowledge of women and men for the same environmental resource may be dissimilar due to different access rights and use of local plants. Other authors who focused on the same high value species in West Africa (Karambiri *et al.*, 2017) illustrated how the classification systems and preferences for shea ethnovarieties vary between gender and ethnic groups. Rimlinger *et al.* (2021a) described how perceptions, preferences and management practices regarding the intraspecific variability of an emblematic African fruit tree species (*Dacryodes edulis*) are shaped by inter-ethnic and rural–urban differences.

Rimlinger *et al.* (2021b) also examined how the social dynamics linked to tree planting (i.e. seed exchange networks) are critical to influence the spatial distribution of genetic diversity, particularly in urban environments where tree seed collected from various sites across the country tend to converge, determining local high levels of genetic diversity. Gachuri *et al.* (2022) investigated the role of social factors in determining use of food tree species in rural households of Central Uganda and Eastern Kenya and consequently affecting food and nutrition security of farming communities. Gender and generational preferences turned out to be very important factors that relate to different levels of ecological knowledge and shape patterns of use of tree resources.

The implementation of strategies for the conservation of forest genetic resources are even more challenging in high-poverty areas, where different users depend on forest resources for their livelihoods and the questions on how to reconcile conservation and livelihood objectives are more pressing. The idea that *in situ* conservation should not exclude use is gaining greater recognition. The concept of ‘other effective area-based conservation measures’ (OECMs) has been recently proposed by IUCN as a new conservation approach that does not coincide with protected areas, and where conservation is resulting from management oriented towards other purposes (IUCN-WCPA Task Force on OECMs, 2019). Larson *et al.*, (2019) proposed to better integrate concerns about rural livelihoods into forest conservation goals and into forest tenure reform policies.

A novel participatory approach to conservation was piloted in 2018, to better understand the effects of climate change on an oak species endemic to California (*Quercus douglasii*), already showing signs of decline, especially at its trailing edge (McLaughlin *et al.*, 2022). Oaks cannot tolerate conventional seed conservation practices, thus participatory field gene banking was tested. This consisted in transplanting individuals from populations of this species located at the trailing edge into a range of distributed plots, in sites corresponding to potential refugia, establishing a network of small common gardens where transplanted individuals would be managed and monitored. The approach appeared to be promising although it would need more testing to determine its effectiveness in assessing adaptation, and ultimately in contributing to conservation. Dawson *et al.* (2014) reviewed evidence about whether commercialization of wild harvested non-timber forest products, or their production under cultivation, could stimulate more sustainable management or reduce pressure on wild stands respectively, but conclusive results on these aspects are missing and more research should be conducted.

6.6 Organization and implementation of *in situ* conservation efforts

After the definition of conservation priorities, the next steps in conservation planning include the actual protection of an area containing the target species and populations, the establishment of a monitoring system, the preparation of management plans for species or forests, the organization of awareness and capacity building activities about the appropriate conservation and use of forest genetic resources (FAO, 2014). In the last decade, *in situ* conservation plans have been developed and reserves have been established at regional and country level and for individual species with different types of distribution, often spreading across multiple countries, therefore requiring coordinated efforts.

In Europe, the principles have been agreed to guide the established of a dynamic conservation framework (Koskela *et al.*, 2013), aiming at conserving genetic diversity of trees, maintaining evolutionary processes and ensuring generational turnover (Lefevre *et al.* 2013). The conservation units that are part of the pan-European network all match a set of minimum requirements (de Vries *et al.*, 2015): they are natural or human-made tree populations where silvicultural interventions are allowed to maintain evolutionary processes and adaptive potential, they are formally identified as conservation units and have a management plan, include one or more species targeted for genetic conservation, have a minimum size to contain a minimum number of reproductive individuals of the target species, are monitored to verify if regeneration is present and if the minimum population size of target species is maintained. More recently, a Forest Genetic Resources Strategy for Europe has been elaborated (EUFORGEN, 2021), extending and strengthening previous efforts, including a greater emphasis on genetic information to guide considerations of what should be conserved and how, increasing concerns about the sustainable use of forest genetic resources and the need for availability and shared access to improved information about forest genetic resources.

In Asia-Pacific, the APFORGEN network has elaborated a strategy to implement the Global Plan of Action on Forest Genetic Resources in the region over the period 2018-2022. The specific objectives include mobilizing political and financial support to implement the Global Plan of Action, making available information on the forest genetic resources in the region, developing conservation and sustainable use strategies for regionally important and threatened tree species, strengthening tree seed supply systems to facilitate ecosystem restoration, and supporting local livelihoods and climate change adaptation and mitigation (APFORGEN, 2018).

In North America, scientists, administrators and conservation practitioners have elaborated reflections on issues and accomplishments in genetic conservation of the tree species in their region (Sniezko *et al.*, 2016), showcasing successful cases and providing guidance for future efforts. These include the experience of Camcore, an international tree breeding and conservation programme based at North Carolina State University, funded by the USDA Forest Service and established in 1980 as a cooperative, with the objective to identify, conserve and collect seed from endangered natural populations of pines found in the natural stands across Mexico, Central America, and the southern United States of America (Jetton *et al.*, 2017; Lopez *et al.*, 2017). The program has played an important role as an international gene conservation cooperative, combining in a complementary manner *ex situ* and *in situ* conservation, and basing its efforts on the knowledge about spatial distribution of diversity of the targeted species. Large part of the material collected has been planted in trials and conservation banks. Seed has also been sent back to the countries where the material has been collected for the establishment of reintroduction studies. Species targeted for seed collection include *Tsuga canadensis*, *Tsuga caroliniana*, *Pinus pungens*, *Chamaecyparis thyoides*, *Picea rubens*, *Abies fraseri* and four rare species of the genus *Fraxinus*. In collaboration with local people, the programme also assessed the conservation status of some of the natural populations targeted, using the criteria established by the International Union for Conservation of Nature (IUCN).

Strategies for individual countries (e.g. for the United Kingdom, Trivedi *et al.*, 2019) and for individual species across multiple countries have been also elaborated (e.g. for *Ulmus* spp. in Europe,

Collin and Bozzano, 2015; for *Fraxinus americana* in North America, Flower *et al.*, 2018, for *Dalbergia cochinchinensis* in Indochina, Hartvig *et al.*, 2022).

Furthermore, basic principles for forest genetic monitoring have been initially proposed to monitor the conservation status of populations conserved within gene conservation units (Aravanopoulos *et al.*, 2015). Later on, forest genetic resources monitoring has been proposed to secure the conservation of the processes that maintain genetic variation in natural populations, especially in the light of climate change (Aravanopoulos, 2016; Fussi *et al.*, 2016), although its inclusion within existing forest monitoring protocols seems to be quite challenging. This is due to different factors such as the high implementation costs, the large number of indicators and verifiers proposed, and the lack of harmonized procedures across countries (Kavaliauskas *et al.*, 2018). The LIFEGENMON consortium, involving researchers from central and southeastern Europe, has tried to address some of the above issues and produced a manual to guide the practical implementation of forest genetic monitoring (Bajc *et al.*, 2020). Indicators to systematically detect loss of genetic diversity have been developed elaborating a national multi-scale assessment of regeneration deficit for tree species across for the United States of America, with the assumption that insufficient regeneration would lead to a progressive loss of genetic variation (Potter and Riitters, 2022). This has been obtained combining data on tree species occurrence and seeds zones and calculating the estimated proportion of small trees (seedlings and saplings) relative to all trees for each species and within seed zone sub-populations. Based on this assessment, ca. 16% of forest tree species in the United States of America seem to be exposed to the risk of losing genetic variation, and this would occur particularly in California and the Southeast of the United States of America, where most of the threatened species are located.

Attempts to assess genetic erosion, defined as the loss of specific alleles, a reduction in richness of the total number of alleles, and a reduction in evenness of the frequencies of alleles in a given place within populations or across species (Quiñones-Pérez *et al.*, 2017), have been carried out also on an endangered endemic species found in Mexico, *Picea chihuahuana*, expected to be highly vulnerable to genetic drift, endogamy depression and strong unidirectional selection, given the small population sizes, with conditions made worse by climatic changes. However, no evidence of genetic erosion was found in the 14 populations studied (Quiñones-Pérez *et al.*, 2017).

With regard to the main challenges affecting implementation of *in situ* conservation of forest genetic resources, an overview carried out by Proschowsky *et al.*, (2020) on genetic conservation of forest trees in Nordic countries of Europe highlighted how constraints vary across countries and how conservation activities are organized differently, particularly regarding the way conservation units are recognized, not having a formal legal status in all countries. Concerns regard particularly the expected impacts of climate change that might challenge ongoing *in situ* conservation efforts, potentially affecting the distribution range of targeted species, or determining a strong selection pressure that eventually may reduce the genetic variation in conserved populations. In the face of climate change and pests and diseases, traditional *in situ* conservation efforts may need to be coupled with additional actions, such as assisted migration, or also cryopreservation. In addition, given the mentioned challenges, interdependence among countries could grow in future, given that national gene pools may need to be supplemented from other countries. Although the ultimate responsibility for conserving forest genetic resources lies with individual countries, international collaboration is likely to become even more critical to ensure *in situ* conservation of forest genetic resources.

6.7 State of *in situ* conservation of forest genetic resources

For the preparation of the present report, 58 countries reported having operational national *in situ* conservation systems in place and two countries reported having initiated the establishment of such a system (Figure 6.1). The list of countries with operational national *in situ* conservation systems is presented in Table 6.1.

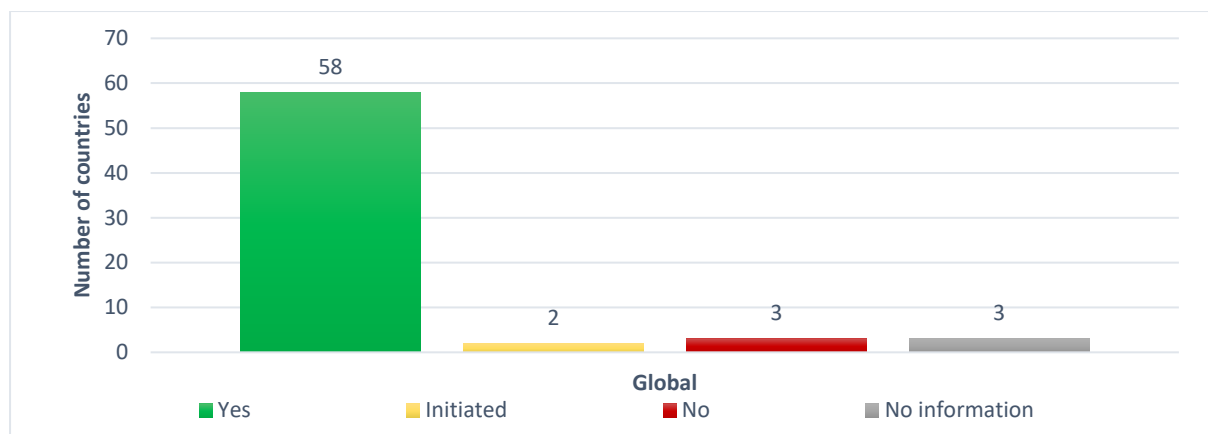


Figure 6.1 Number of countries with operational national *in situ* conservation systems.

Table 6.1 List of countries with operational national *in situ* conservation systems.

Region	Countries
Africa	Burkina Faso, Ethiopia, Guinea, Kenya, Madagascar, Mauritania, Morocco, Namibia, Niger, South Africa, Zimbabwe
Asia	China, Japan, Republic of Korea, Lao People's Democratic Republic, Sri Lanka, Thailand
Europe	Austria, Bulgaria, Croatia, Cyprus, Czechia, Denmark, Estonia, Finland, France, Georgia, Germany, Greece, Iceland, Ireland, Italy, Lithuania, Luxembourg, Malta, Netherlands, Norway, Poland, Portugal, Russian Federation, Serbia, Slovenia, Spain, Sweden, Switzerland, Türkiye, Ukraine
Latin America and the Caribbean	Argentina, Brazil, Chile, Ecuador, Mexico, Saint Lucia
Near East	Lebanon, Yemen
North America	Canada
Southwest Pacific	Australia, Fiji

In 2012, 47 countries had established national *in situ* conservation systems (Figure 6.2). Between 2012 and 2019, five countries (Luxembourg, Malta, Mexico, Spain and Sweden) reported the establishment of such a system. Since 2019, no new national *in situ* conservation systems have been established. Of the 58 countries with national *in situ* conservation systems, six were unable to report the establishment year.

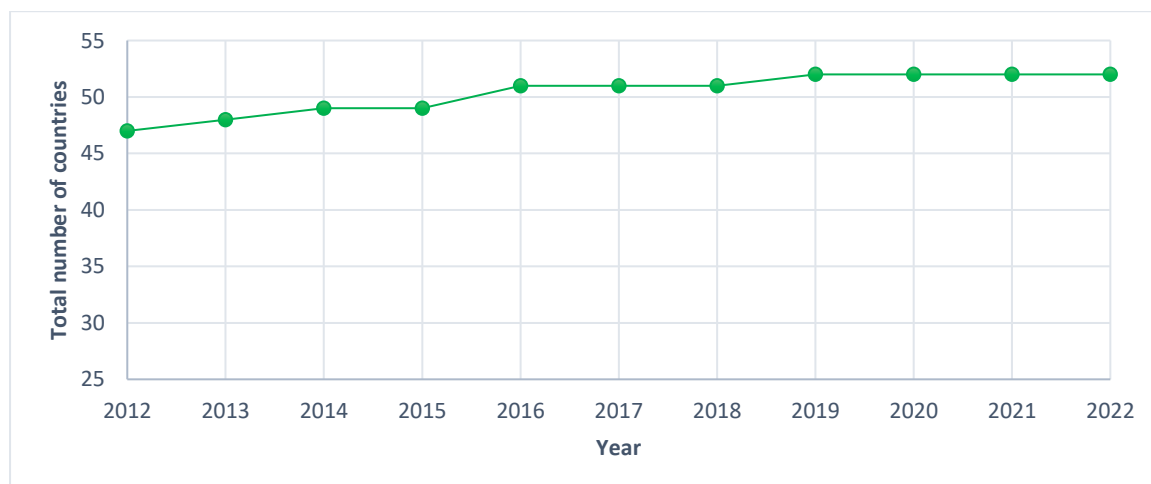
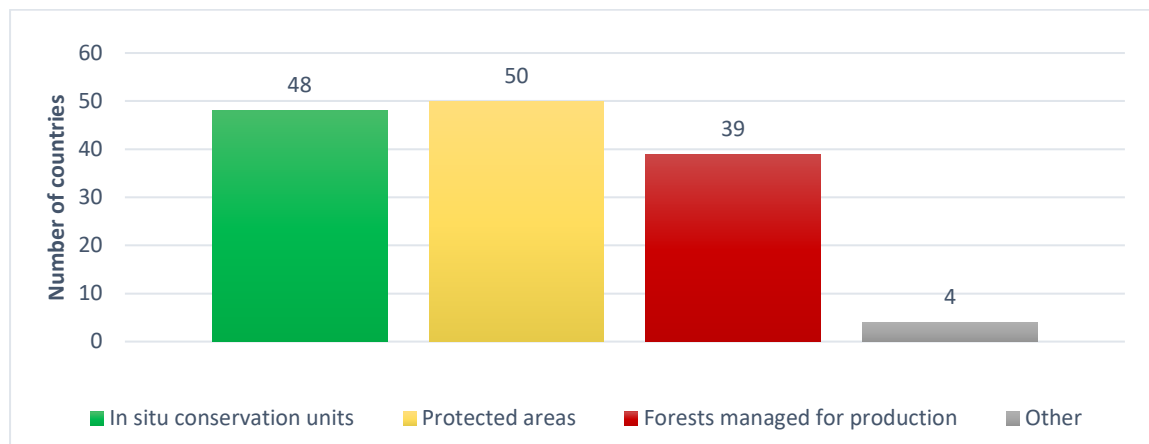


Figure 6.2 Development of the national *in situ* conservation systems in 2012–2022.

The most common components of the *in situ* systems were protected areas (reported by 50 countries) and *in situ* conservation units of FGR (48), followed by forests managed for production of wood and/or non-wood products (39) (Figure 6.3). Four countries reported other components (e.g. permanent monitoring or research plots and sacred forests) being included in their *in situ* systems.

**Figure 6.3** Different components of the national *in situ* conservation systems.

For this report, the countries reported 25 618 *in situ* units with a total area of over 108 million hectares. The reported *in situ* conservation programmes include 1 283 species which represent only about two percent of the world’s tree and other woody species. The number of species in these programmes was highest in Latin America and the Caribbean (470), followed by Asia (337) and Europe (208) (Table 6.2). However, the number of species covered by *in situ* conservation is likely to be much higher because the genetic conservation of trees and other woody species in protected areas and elsewhere remain poorly documented. According to the GlobalTree Portal²¹, 34 976 (60%) of the world’s trees are found in at least one protected area globally.

Table 6.2 Number of species, by region, included in *in situ* conservation programmes.

Region	Number of species*
Africa	157
Asia	337
Europe	208
Latin America and the Caribbean	470
Near East	36
North America	117
Southwest Pacific	47

* Net number of species reported by region

6.8 Conclusions

Threats to forest ecosystems may not necessarily lead to species loss but rather to the disappearance of some populations that could host critical and unique traits. Therefore, a proper characterization of intraspecific diversity and the implementation of conservation actions at population level is crucial. Spatial analyses of threats so far conducted have revealed that a small part of the genetic diversity of tree species is currently included within protected areas.

The principles guiding *in situ* conservation of forest genetic resources from the 1980s are still generally valid and no major methodological revolution has taken place, but conservation efforts can

²¹ <https://www.bgci.org/resources/bgci-databases/globaltree-portal/>

now benefit from new genomic tools with higher detection power. Genetic and genomic data are available for many more species compared to 10 years ago, range-wide characterizations of tree species' genetic diversity are accumulating, improving knowledge of where to concentrate *in situ* conservation efforts of genetic resources.

Scientific understanding of threats (including resistance to pathogens) and adaptive processes has also advanced significantly, particularly due to genomic data that have enabled to examine the extent of local adaptation, at individual and population level, and to find traces of adaptation also over very small spatial scales. Furthermore, approaches based on transcriptomic, proteomic and metabolomic data have been adopted to investigate highly complex traits. These methods, in combination with genome-wide variation data, enabled to explore causal linkages between genotype and phenotype, through statistical modeling.

The increased capacity to generate genetic and genomic data, and to link them to environmental and phenotypic data, has led to more powerful modeling efforts. This allows to better define what is being conserved *in situ*, whether conservation is effective, whether active management is needed to ensure conservation and what is happening at landscape scales where exchanges of geneflow are taking place between protected areas and those outside. Moreover, what has emerged clearly in the last decade is that *in situ* conservation also needs to include the use of forest genetic resources

Even though individual countries are ultimately responsible for conserving their forest genetic resources, international collaboration is likely to become even more critical to ensure *in situ* conservation of forest genetic resources in the face of climate change and pests and diseases. National gene pools may need to be supplemented from other countries, and therefore interdependence among countries is likely to continue increasing in the future.

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CHAPTER 7. *EX SITU* CONSERVATION OF FOREST GENETIC RESOURCES

7.1 Introduction

The development of appropriate *ex situ* conservation methods for forest genetic resources that are connected to practical tree planting and management have never been more crucial. Massive planned activities on forest and landscape restoration in the coming decades have only increased in importance since the first State of the World's Forest Genetic Resource Report (FAO, 2014). These activities require access to tree seed and the knowledge that comes from *ex situ* storage and research based on these tree seed stocks (Box 7.1). Recent and prominent calls from researchers and practitioners have stressed the need for more *ex situ* tree seed banks that contain 'active' as well as 'conservation' stocks to support restoration (Goodale *et al.*, 2023). With increased climate change impacts on forests that limit *in situ* conservation opportunities, including disease- and fire-mediated effects (Alfaro *et al.*, 2014), more emphasis on *ex situ* conservation is also needed. Again, the increased recent recognition of the need to diversify food systems to support environmental resilience and benefit consumers' health mean that greater availability of food trees is required (Ickowitz *et al.*, 2022), whose promotion entails access to *ex situ* conserved seeds and seedlings. Access to the germplasm of these food trees is needed to conduct research on them so that they are able to fit better into new anthropic production system outside traditional wild-managed production.

On top of the above, ongoing forest conversion to agriculture, a long-standing problem, demands that *ex situ* storage methods are increasingly optimised to conserve forest genetic resources as the opportunities for conservation in natural systems wane (e.g., Stévant *et al.*, 2019). This is particularly so for parts of the world where forest losses to crops and pastureland is high, and where there are high levels of tree endemism (see Chapter 4). Globally, over 20 000 tree species of the known roughly 60 000 species (Beech *et al.*, 2017) – that is, over 30 percent of all tree species – are by some accounts considered threatened (BGCI, 2023). It is not only the species that are being lost, but, crucially, the genetic diversity within them. Conserving trees and using them effectively is much more than just preserving an example or two of each species. This would be useless as most tree species are outbreeding and therefore need other trees to set good-quality seed for the next generation. In this conservation, the continued evolution of trees to respond to new environments created by climate change and anthropic landscapes more broadly must increasingly be considered.

From a forest and landscape restoration perspective, tree planting (along with managed natural regeneration) is an important approach for supporting restoration. However, the lack of access to a diverse range of tree species and genetic resources, matched appropriately to environments and planters' needs, and of the appropriate physiological quality, has been an important factor in limiting current restoration success (Jiang *et al.*, 2016; Yao *et al.*, 2016; Xiao *et al.*, 2020; Nunes *et al.*, 2020; Palmer and Stewart 2020). Instead, what gets planted is simply whatever tree seeds and seedlings can be found, irrespective of how suitable these are – and they are often highly suboptimal – for meeting planting goals. Too few tree species have been planted in restoration initiatives, with often a predominant focus on exotic trees in the absence of other planting materials, of the wrong provenance, and without much consideration of the needs of local communities (Jalonen *et al.*, 2018). Unless progress is made, widely publicised recent failures in tree planting may mean that civil society and potential planting investors begin to question whether engaging in such 'restoration' is appropriate (Jones, 2021).

To achieve progress, more focus is required on developing conservation methods *ex situ* that can be applied to a broad diversity of tree species, on the linking of these methods to the appropriate characterisation of germplasm, and, crucially, on more effectively linking this conservation to the tree seed and seedling supply systems that actually provide planting material to growers. This last aspect is crucial as a major criticism of storing tree seed in genebanks is that it becomes inaccessible for use by growers (Dawson *et al.*, 2013). To properly meet germplasm supply needs for good-quality, locally adapted and diverse tree planting material, existing tree conservation and local seed and seedling supply value chains need to be strengthened to provide better access (Graudal *et al.*, 2021). This is especially true for native trees, for which current seed and seedling sources do not exist practically, or those that do are difficult to access and have not been genetically tested for their productivity,

economic and other relevant values. The physiological quality of the seed is also an important factor, meaning that progress in seed storage that enhances this quality is a necessary consideration (Pritchard *et al.*, 2014).

The way that tree genebanks need to operate to conserve, genetically develop and supply high-quality tree seeds and seedlings for planting is very different to how genebanks for annual crops work. This is primarily because, unlike with annual crops, there is generally no clear distinction for trees between conservation, breeding and deployment to growers (Dawson *et al.*, 2013). This is because of the much longer time it normally takes for trees to mature and produce seed, which means that genetic improvement and the production of tree planting materials must generally be combined with the conservation process, rather than following an ‘in series’ approach typical for annual crops. This explains why field as well as seed genebanks have critically important roles to play for trees. When established in secured locations, field genebanks can conserve the trees, can be evaluated to support selection and breeding by taking advantage of low-input breeding methods, and can produce seeds and seedlings to meet restoration and other planting targets (Graudal *et al.*, 2021, 2022). Tree seed and field genebanks are interconnected through a cycling of material in which field genebanks are established from seed genebanks, and seed from field genebanks is returned to seed genebanks when this becomes possible.

Field genebanks are also particularly crucial for tree conservation, genetic development and supply for the many species that have recalcitrant seed that is unable to be stored and remain viable for any length of time and/or because, for some trees, vegetative propagation methods are used to maintain ‘true-to-type’ selected individuals with superior traits. Connected with these considerations is the observation that tree seeds are physiologically different from those of cultivated annual crop plants because they have not been through the same processes of domestication as the latter have, which have involved changes in seed properties such as dormancy, viability and the permeability of the seed coat, all of which can have a positive impact on seed storage behaviour. The lack of domestication of most trees also means that much more variation can be exhibited within species in traits such as phenology and seed characteristics, making initial collection and storage harder.

These special features of trees explain why tree genebanks activities are sometimes structured differently, and are broader, than those of classic crop genebanks, and why substantial investments in research to devise appropriate *ex situ* storage methods is required. This involves connecting basic biological research on tree seeds with the socio-economic context of users and society, to justify increased investment.

In this chapter, the different methods for the *ex situ* conservation of tree genetic resources are reviewed and progress related. For current purposes, we consider *ex situ* conservation to cover seed and live field genebanks of trees (the two most common methods of *ex situ* conservation for trees), as well as other methods of *ex situ* storage including cryopreservation and *in vitro* conservation. Not included is the conservation of trees in human production landscapes, such as farmers’ fields, which for trees occupy an intermediate position between *in situ* and *ex situ* conservation that is classically referred to as *circa situm* conservation, where human management and natural interventions operate together (Dawson *et al.*, 2013). However, the distinction between *ex situ* and *circa situm* conservation can sometimes become blurred when tree seed production stands that also have conservation functions are located on growers’ land.

Box 7.1 Some forest and landscape restoration tree planting initiatives that extensively rely on the provision of tree genetic resources

Massive planned forest and landscape restoration activities in the coming decades require access to tree seed and the knowledge that comes from *ex situ* storage and research based on these tree seed stocks. Some examples of the overlapping initiatives that require these inputs are listed below.

The Bonn Challenge (<https://www.bonnchallenge.org/about>). The Bonn Challenge is the global effort to bring 350 million hectares of degraded and deforested landscapes into restoration by 2030. Programmes that link with the Bonn Challenge include the African Forest Landscape Restoration

Initiative (AFR100); Initiative 20x20 in Latin America and the Caribbean; ECCA30 in Europe, the Caucasus and Central Asia; and the Agadir Commitment in the Mediterranean region.

The World Economic Forum's Trillion Tree Initiative (1t.org; <https://www.1t.org/>). Designed to support the UN Decade on Ecosystem Restoration of 2021-2030, 1t.org originated as part of the World Economic Forum's commitment to accelerate nature-based solutions to solve the climate crisis. The initiative, which has the objective of planting one trillion trees all over the world, acts through its five chapters of the United States of America; the Sahel and Great Green Wall; the Amazon Basin; India; and China.

One Tree Planted (<https://onetreepanted.org/pages/about-us>). With a simple vision of "one dollar for one tree", since 2014 the foundation has planted 40 million trees in 47 countries as an official reforestation partner of the United States Forest Service.

Plant a Billion Trees (<https://www.nature.org/en-us/get-involved/how-to-help/plant-a-billion/>). Launched in 2008, this large-scale restoration project coordinated by The Nature Conservancy aims to plant a billion trees particularly in the Mexican Mayan forest and the Brazilian Amazon.

Tree Nation (<https://tree-nation.com/>). Through 94 planting projects, the organisation has planted 21 million trees from 300 different species, primarily promoting local trees to benefit local communities as well as the environment.

The International Tree Foundation (<https://www.internationaltreefoundation.org/>). The foundation started planting trees in 1922. Since 2012 it has planted more than five million trees in 100 countries.

7.2 Methods for *ex situ* conservation and progress achieved

7.2.1 Seed genebanking

Seed genebanking is historically one of the most followed, economic, and practical method of conservation, where dried seeds are stored in sealed containers under cold, hygienic and secured conditions, from where they can be accessed in the future for characterisation, regeneration and distribution. The method is suitable for those tree seeds (so-called 'orthodox' seeds) that can substantially withstand desiccation and cold conditions. Conservation collections of tree seeds can store tremendous amounts of inter- and intra-specific diversity in a relatively inexpensive manner and in a small space. During the process of drying, the seeds enter a quiescent stage where metabolic processes are reduced almost to a standstill. To continue in this state, low relative humidity and temperatures delay the process of physiological aging. Orthodox tree seeds can be stored at 3% to 7% moisture content at 5 degrees Celsius for up to 5 years or at minus 20 degrees Celsius for 20 years and above (De Vitis *et al.*, 2020). As might be expected, the storage behaviour of tree seeds is better known for common, temperate tree species than it is for more locally distributed, tropical trees (Wyse and Dickie 2017; Wyse *et al.*, 2018).

Perhaps counter-intuitively with the expansion of the internet, the coordinated availability of knowledge on what tree species are actually stored in 'active' as well as 'conservation' stocks globally has declined in recent decades. Previously, genebanks and seed suppliers were willing to provide physical catalogues on request that listed their stock, and this allowed the compilation of the paper-based Tree Seed Suppliers Directory (TSSD) in 1997 (subsequently converted to an online version; <https://www.worldagroforestry.org/output/tree-seed-suppliers-directory>) using information from 144 commercial suppliers and/or genebanks. In an attempted update of the TSSD in 2015, it proved impossible to obtain the same level of information from suppliers in paper form, nor was it possible to simply 'scrape' information from multiple online information sources. The inability to update the TSSD leaves a significant gap in the current understanding of what tree seeds are stored and available for use globally.

Predicting seed storage behaviour

The fundamental Ellis and Roberts (1980) equation provides the basis for predicting seed longevity under storage conditions for orthodox seeds and has been widely used in the last decades to derive seed viability constants and ‘standards’ for trees (e.g., Dickie and Bowyer 1985; Dickie *et al.*, 1990; Fantinatti and Usberti 2007). The equation remains very helpful for modelling seed longevity of plant seeds where it is impossible to individually research all species that need to enter seed storage, as is the case for tree species, especially tropical ones. It also allows the identification of discrepancies between predictions and actual storage performances that require further research (Solberg *et al.* 2020). Recent studies of the seed viability of six European trees (*Malus sylvestris*, *Pyrus communis*, *Sorbus aucuparia*, *Prunus avium*, *Prunus padus* and *Cornus sanguinea*) concluded that species with deeper physiological dormancy (*S. aucuparia*, *P. padus* and *C. sanguinea*) tended to be more tolerant of desiccation and low temperatures (Wawrzyniak *et al.*, 2020). In their study on five tropical forest tree species (*Chamaedorea glaucifolia*, *Cymbopetalum baillonii*, *Magnolia mexicana*, *Nectandra coriacea* and *Ternstroemia tepezapote*) from south-eastern Mexico, Becerra-Vázquez *et al.* (2018) reported that seed longevity was related to various functional and ecological traits, along with the prevailing weather conditions at the time of seed dispersal. Accelerated ageing tests, conducted at higher temperatures and relative humidities than standard storage conditions, are a way of mimicking the ageing process of seeds in storage. Recent tests conducted on seeds of 22 UK woody species native to the United Kingdom indicated taxonomic trends in storage behaviour, but that caution was needed in making broad conclusions on potential seed storage life at species, genus and family levels (Davies *et al.*, 2020).

Associations observed between desiccation tolerance and habitat, agroecological zones, phylogeny and seed traits (Ellis *et al.*, 2007; Hamilton *et al.*, 2013; Pritchard *et al.*, 2014; Obroucheva *et al.*, 2016; Wyse and Dickie, 2017), among other factors, have been used to develop more advanced mathematical models for predicting seed storage behaviour. One of the first multi-variable probabilistic prediction models that was applied used measures of seed mass (SM), moisture content (MC), seed coat ratio (SCR) and rainfall in the month of seed dispersal for 104 species from 37 families from a semi-deciduous tropical forest in Panama (Daws *et al.*, 2006). A binary logistic regression predicted desiccation intolerance for seeds with large mass and thin seed coats with reasonable accuracy. This SCR-SM model was also used for successfully predicting the seed desiccation tolerance of woody species from the Xishuangbanna tropical rainforest in Yunnan Province of southern China (Lan *et al.*, 2014). Another model fitted to 195 diverse species used ecological correlates to predict that endospermic seeds of early angiosperms which evolved in forest understorey habitats are short-lived (Probert *et al.*, 2009).

To understand more about the global distribution of recalcitrant- and orthodox-seeded plant species, Wyse and Dickie (2017) studied the available information in Kew's Seed Information Database (Royal Botanical Gardens, 2022) for 17 378 taxa of which 643 were considered desiccation-sensitive and 16,605 desiccation-tolerant, building independent prediction models based on taxonomic relatedness and habitat distribution. They found that taxonomic prediction worked well for lower levels of taxonomic relationships but, as would be expected, at higher taxonomic levels the model started to show discrepancies. Their habitat-based prediction model showed fewer variations compared to the taxonomy-based model. Overall, both models were useful for predicting seeds' desiccation response. Using taxonomic affinity, habitat and seed mass for 17 539 plant species, Wyse and Dickie (2018) further fitted regression model to predict seed desiccation response with more or less similar outcomes. The most important predictor variables were the seed desiccation responses of a species' relatives, seed mass and annual precipitation.

Although not yet tested on tree species, another model which uses deep learning (high-end artificial neural network analytics) and red-green-blue (RGB) imaging technology has been proposed to predict the germination responses of commercial vegetable species seed lots (Nehoshtan *et al.*, 2021). The 2021 study involved a training seed lot with known outcome and a test seed lot for testing the predictive outcome, resulting in $\geq 90\%$ precision. Such new computational methods based on machine learning may also be useful for predicting the germination responses of tree seeds.

Understanding desiccation intolerance as a key issue in seed conservation

Sensitivity to seed desiccation that results in recalcitrance remains one of the prime concerns for tree seed conservation as it can severely limit possible storage life. Around 80% of trees of Asian origin were found to be recalcitrant compared to 8% of African origin (Kettle, 2012; Umarani *et al.*, 2015). The Dipterocarpaceae family was found to have 98% recalcitrant species, whereas Malvaceae, Rubiaceae, and Bignoniaceae had less than 10% (Umarani *et al.*, 2015). Among the Amazonian forest species, around 60% have been reported to be recalcitrant (Pritchard *et al.*, 2014). The Seed Information Database (Royal Botanical Gardens, 2022), as already mentioned above and first released in 2001, is still a primary source of seed desiccation-sensitivity data and contains information for over 18 000 taxa, but it is heavily biased towards desiccation-tolerant temperate plants (Wyse and Dickie, 2017). In the last decade, some studies that have tried to redress the balance by focussing on understanding the seed storage behaviour of tropical species include Waiboonya *et al.* (2019) (for North Thailand), Mattana *et al.* (2020) (for the Caribbean) and Lima *et al.* 2014 (for the Amazon).

The physiology of recalcitrance is still not a well-studied phenomenon, but there seem to be three biological reasons for the reductions in seed viability (Umarani *et al.*, 2015). Cellular mechanical damage due to vacuolar collapse of cellular organelles during drying may be one cause. The embryos of recalcitrant seed have a large proportion of vacuoles within the cells and a positive correlation is observed between vacuolation and recalcitrance (Farrant *et al.*, 1992, 1997). Metabolism-induced damage, where the seeds do not stop or reduce their metabolic processes despite reductions in water content, are another possible cause. This leads to the generation of lethal free radicals and reactive oxygen species (ROS) (Chandra and Keshavkant, 2018; Kurek *et al.*, 2019) that have been highlighted as a prime reason for the reduction of seed viability of orthodox seeds (Zhang *et al.*, 2021). A third reason relates to the failure to de-differentiate cellular organelles during the process of maturation drying (Umarani *et al.*, 2015). Late embryonic abundant (LEA) proteins, specifically the dehydrins, can impart desiccation tolerance and are known to be synthesized during the process of embryogenesis and maturation in orthodox seeds, but their role in determining storage behaviour appears complicated (Azarkovich, 2016).

Increasingly advanced genomic approaches provide opportunities to understand the genetic and molecular components of plants' seed storage behaviour. A study examining 86 reports from diverse annual plants, for example, summarised the roles of multiple quantitative trait loci (QTLs) and genes (transcription factors, hormonal and signaling pathway genes, seed storage proteins, etc.) involved in seed ageing processes (Arif *et al.*, 2022). In Chinese cork oak (*Quercus variabilis*), a differential gene expression study revealed more than 4 000 genes to be significantly affected by seed desiccation over a period of 15 days (Li *et al.*, 2021). Affected were heat shock family proteins, LEA proteins, hormone related genes (abscisic acid and auxins), plant hormone signal transduction pathways and glycerophospholipid metabolism genes.

High-throughput proteomics have been used to functionally understand tree seed desiccation behaviour. In holm oak (*Quercus ilex*), a study comparing the protein profiles of different embryonic regions indicated a high-level of protein compartmentalisation among different parts of the embryo (Sghaier-Hammami *et al.*, 2015). Among the 226 differentiated proteins, the embryonic axis had significantly higher amounts, as well as a more highly diverse set of proteins, than cotyledons and the tegument, whereas the tegument had high representation of stress and defence-related proteins, albeit far less in comparison to the embryo axis. In another proteomic analysis of germinating embryos in the same species, 153 differentially-expressed proteins were revealed (Romero-Rodríguez *et al.*, 2019). Although these studies do not provide a full picture of desiccation intolerance in recalcitrant tree seeds, they do open up new avenues to look at this poorly-studied phenomenon, using combinatorial transcriptomic and systems biology approaches. More such studies are needed for trees, as their results could support augmenting seed longevity by external chemical applications or physical treatments as well as by optimising basic storage conditions.

Field genebanking

As noted above, seed genebanking is not the *ex situ* conservation method most suited for many tree species that produce recalcitrant seeds or that are propagated vegetatively to maintain true-to-type lines (important for many fruit tree species). A high proportion of threatened tree species are recalcitrant, so establishing field genebanks of these species is therefore one priority (Wyse *et al.*, 2018). In addition, since the production of tree planting materials must be combined with the conservation process, field genebanks of orthodox tree species too have critically important roles to play. Field genebanks, if appropriately designed and managed, can play the multiple functions simultaneously of conserving trees, evaluating genetic variation to support selection and low-input breeding, and producing seeds (and seedlings and clones) to meet restoration and other planting targets (Graudal *et al.*, 2021, 2022). As noted above, this is especially and increasingly important for tree seed supply for large-scale forest landscape restoration projects. With advances in the more holistic ‘systems approach’ to tree breeding known as ‘tree diversity breeding’, field genebanks that double up in the evaluation of tree germplasm have new and particular roles to play (Hendre *et al.*, 2022). The concept of tree diversity breeding has recently been formalised and is described in Box 7.2 along with the implications of the approach for tree field genebanking.

Currently, the majority of live *ex situ* conservation collections of trees are held by botanical gardens. Botanic Garden Conservation International (BGCI) maintains a database of botanical institutes (https://tools.bgci.org/garden_search.php) that includes around 800 well-established botanical gardens that are estimated to harbour around 60 000 to 80 000 plant species in total (as seed and live plants; O’Donnell and Sharrock, 2017). But often the number of ‘live’ individuals per plant species is low in botanic gardens because of the expense needed to maintain larger live collection, especially when considering trees. This is a problem for the regeneration of live tree collections as most trees are predominantly outbreeding and suffer from inbreeding depression. On the other hand, CIFOR-ICRAF is one institution that maintains with partners a network of diversified field genebanks of agroforestry tree species where emphasis is placed on the within species representation of diversity (<http://apps.worldagroforestry.org/products/grunew/>).

Many botanic gardens also suffer from the absence of plausible routes by which the tree genetic resources they conserve – whether as seed or live collections – can be ‘repatriated’ to support biodiversity in the natural and working environments of forests and woodlands, forestry and agroforestry (Dawson *et al.*, 2013). Rather, their primary value is in better understanding the tree species in order that they can be appropriately managed for seed collection, seed storage, production, etc., in other initiatives. A new global partnership platform spearheaded by BGCI to strengthen arboreta, called “ArbNet”, was established in 2017 to fund international collaborations between tree-focused botanic gardens and arboreta for the purpose of exchanging skills, resources and expertise to advance tree conservation efforts (<http://arbnet.org/bgciarbnet-partnership-programme>).

A recent resurgence of interest in the design and planting of breeding seedling orchards (BSOs) (Barnes, 1995) is connected to the need to conserve, evaluate and supply tree genetic resources within integrated tree seed and seedling systems that cater for large-scale tree planting initiatives (Graudal *et al.*, 2021). A good recent example, where over 30 BSOs have been established, is the ongoing Provision of Adequate Tree Seed Portfolios (PATSPPO) project in Ethiopia (<https://www.worldagroforestry.org/project/provision-adequate-tree-seed-portfolio-ethiopia>) that has been designed to support Ethiopia’s massive landscape restoration target of 15 Mha by 2030. These BSOs allow different provenances of the trees to be assessed while conserving and supplying seed, and can take account of future climate trends in determining appropriate seed sources for specific locations.

The key challenge is to scale up and out the lessons learnt in PATSPPO to other African countries and more widely, especially for native tree species. This involves understanding the challenges and trade-offs involved in combining multiple functions into BSO management, particularly conservation and improvement functions, and modelling to national governments the benefits that BSOs can bring compared to the investments required in their establishment and management (Pedercini *et al.*, 2022). Innovative tools combining statistics, ecological genomics (the use of genomics to understand natural variation in relation to the environmental variables and adaptive performance of trees) and genome-

based field selection (use of genomics to associate traits of importance in replicated experimental trials), can be very helpful in maintaining a balance between conservation and productive functions.

Box 7.2 Tree diversity breeding and the implications for tree field genebanks

Trees have roles in countering many key planetary health concerns and this means they provide an excellent example of where a systems approach to plant breeding, in which social, environmental, technological and economic trends – and their associated perspectives, concerns and values – are considered together, is important for addressing global challenges effectively. Building links between different tree breeding methods responsive to different existing trends has been labelled as ‘tree diversity breeding’ and the concept was explained more fully by Graudal *et al.* (2022). These authors explained the approach by considering pairwise combinations of four key global trends related to *participation*, *environment*, *biotechnology* and *markets*. They suggested the use of citizen science tree breeding approaches to bridge *participation* and *environment* trends; new statistical approaches to support progress in the understanding of trees’ genetic adaptation to bridge *environment* and *biotechnology* trends; the manipulation of tree product quality/processability-related genes to bridge *biotechnology* and *markets* trends; making use of advances in production system modelling of tree varieties to bridge *markets* and *participation* trends; the manipulation of tree architecture-related genes (and other genes that determine the labour costs of tree production) to bridge *participation* and *biotechnology* trends; and the use of novel methods to explore genetic, tree product quality and production system design relationships to bridge *environment* and *markets* trends.

Hendre *et al.* (2022) specifically looked at the implications of tree diversity breeding for organisations such as CIFOR-ICRAF that work at the agriculture–forest interface, as well as for institutions that engage in *ex situ* tree genebanking activities. The adoption of the approach requires a change in emphasis in the breeding values that are considered important in genetic improvement and this will affect the design and operation of tree field genebanks that also support selection and breeding in at least two regards.

First, *the types of traits* characterized in field genebank evaluations requires new thought, with increased importance being given to traits that support environmental service provision and environmental fitness, and that determine product quality and the labour costs of tree production. Specific traits that may require more attention include tree architecture and phenology, both of which determine how good a tree is in providing environmental services and both of which may affect the labour costs (or the timing of labour inputs) of production.

Second, *the design of stands* will need to change to support more holistic, systems-based evaluation. Instead of only planting single-species genebanks, multi-species stands may sometimes be required. This will enable an exploration of the interactions between tree species, or even between trees and important annual crops. This new approach to genebank design would allow the role of genetics in defining new, integrated production systems to be better defined. In addition, if designs for mixed-species breeding seedling orchards and the like are drawn up and implemented correctly, it should not (or at least not markedly) detract from the conservation and propagule supply functions of the stands.

From the perspective of policy, the starting point for the wider adoption of the tree diversity breeding approach is to ensure that tree breeding does not only focus on the traditional metrics of productivity and (companies’) profitability as measures of breeding advancement. Rather, for a systems approach to tree breeding to be successful, a broad set of measures that define breeding success is required. These should include aspects of resilience, sustainability, nutritional security, local culture and conservation. In each case, appropriate values and measures of success need to be defined and adopted by the relevant stakeholders. Policy interventions to encourage a systems approach to tree breeding should provide incentives for tree researchers and breeders to embrace these broader values.

7.2.2 Other methods of *ex situ* conservation

Cryopreservation is a technique that conserves vegetal structures at very low temperatures, such as in liquid nitrogen (minus 196 degrees Celsius), where all cellular and physiological processes are arrested. The plant material is processed in cryogenic material before storage to prevent tissue damage. Pollen, seeds, shoot tips, dormant buds, cell suspensions, embryonic cultures, somatic and zygotic embryos, and callus tissue, can also be stored, but the approach is technically and financially demanding (Engelmann, 2012; Benelli *et al.*, 2013). It however provides opportunities for the conservation of recalcitrant trees. Most work has been on commodity tree crops rather than forest tree species, so work on the tree commodities still needs to be translated to a broader range of trees. In avocado (*Persea americana*), different plant materials such as somatic embryos and shoot tips have been successfully preserved (O'Brien *et al.*, 2021). In coffee (*Coffea arabica*), zygotic embryos have been preserved using droplet-vitrification or encapsulation–vitrification protocols without dehydration (Valdés *et al.* 2021). Cryoprotected shoot tips of 32 citrus taxa were preserved and revived, with varying success rates (Volk *et al.*, 2017). The somatic embryos of cocoa (*Theobroma cacao*) have also been preserved and successfully revived (Adu-Gyamfi *et al.*, 2016, 2020), and holm oak (Barra-Jiménez *et al.*, 2015). Overall, cryopreservation of the embryo axis remains the best method for preserving recalcitrant tree seeds but the approach remains resource intensive, technologically demanding, and experimentally challenging (Berjak and Pammenter, 2017).

In vitro conservation embraces tissue culture methods where a plant is stored and maintained under artificial conditions of temperature, nutrition and water. These include conditions of normal growth, slow growth and arrested growth, as well as other modifications of plant tissue and organ culture. Many temperate trees and nuts, such as those belonging to *Malus*, *Morus*, *Prunus*, *Punica* and *Pyrus*, have been conserved using different *in vitro* techniques including slow culture, cell culture, shoot culture and shoot tip culture, with varying success rates (Reed, 2020). Using growth-retardant medium, date palm somatic embryos were successfully stored under slow growth conditions (Hassan, 2017). In another study, slow growth cultures for *Prunus*, *Punica*, *Ficus*, *Cydonia*, *Pyrus*, *Malus*, *Eriobotrya* and *Crataegus* were successfully tested (Arbeloa *et al.*, 2017). This progress needs expanding to other trees.

Tree DNA banking can tangentially be considered as a method of germplasm conservation as information that can be extracted through sequencing using molecular biology methods can be used for purposes such as gene editing (Bewg *et al.*, 2018). The long-term storage of DNA in banks requires special provisions in terms of storage, access, retrieval and documentation, in order to maintain DNA integrity. The global Genesys plant genetic resources platform contains 648 records of forest genetic resources being stored in DNA banks, for 33 species (<https://www.genesys-pgr.org/>; November 2022 figures).

7.3. The state of *ex situ* conservation of forest genetic resources

For the preparation of this report, 51 countries reported having operational national *ex situ* conservation systems in place and seven countries reported having initiated the establishment of such a system (Figure 7.1). The list of countries with national *ex situ* conservation systems is presented in Table 7.1.

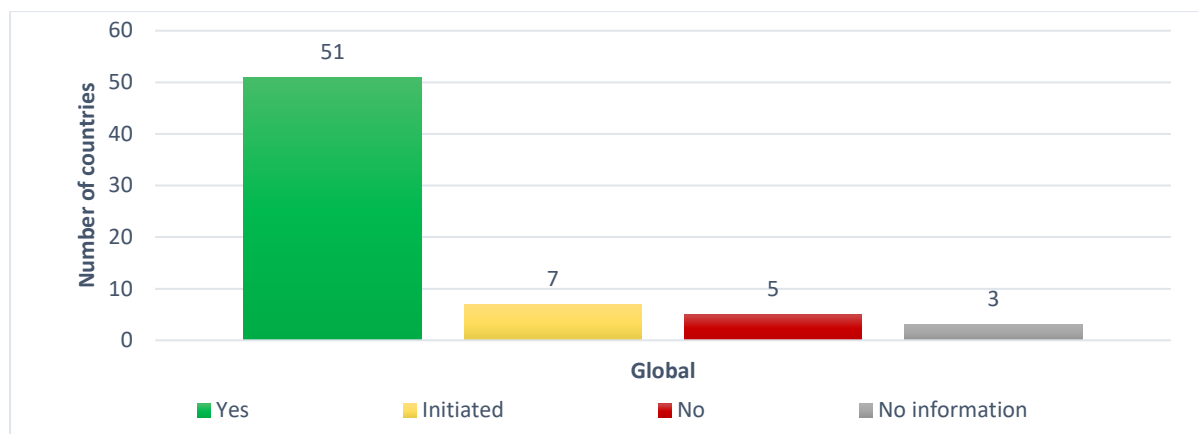


Figure 7.1 Number of countries with operational national *ex situ* conservation systems.

Table 7.1 List of countries with operational national *ex situ* conservation systems.

Region	Countries
Africa	Burkina Faso, Ethiopia, Guinea, Kenya, Madagascar, Morocco, Namibia, South Africa, Zimbabwe
Asia	China, India, Japan, Republic of Korea, Lao People's Democratic Republic, Sri Lanka, Thailand
Europe	Austria, Belgium, Croatia, Cyprus, Czechia, Denmark, Estonia, Finland, France, Germany, Greece, Ireland, Italy, Lithuania, Luxembourg, Netherlands, Norway, Poland, Portugal, Russian Federation, Serbia, Slovenia, Sweden, Switzerland, Türkiye, Ukraine
Latin America and the Caribbean	Argentina, Chile, Ecuador, Mexico
Near East	Iran (Islamic Republic of), Yemen
North America	Canada
Southwest Pacific	Australia, Fiji

The most recent national *ex situ* conservation system was established in Mexico in 2011, and since 2012 no country has reported the establishment of such a system (Figure 7.2). Of the 51 countries with national *ex situ* conservation systems, five were unable to report the establishment year.

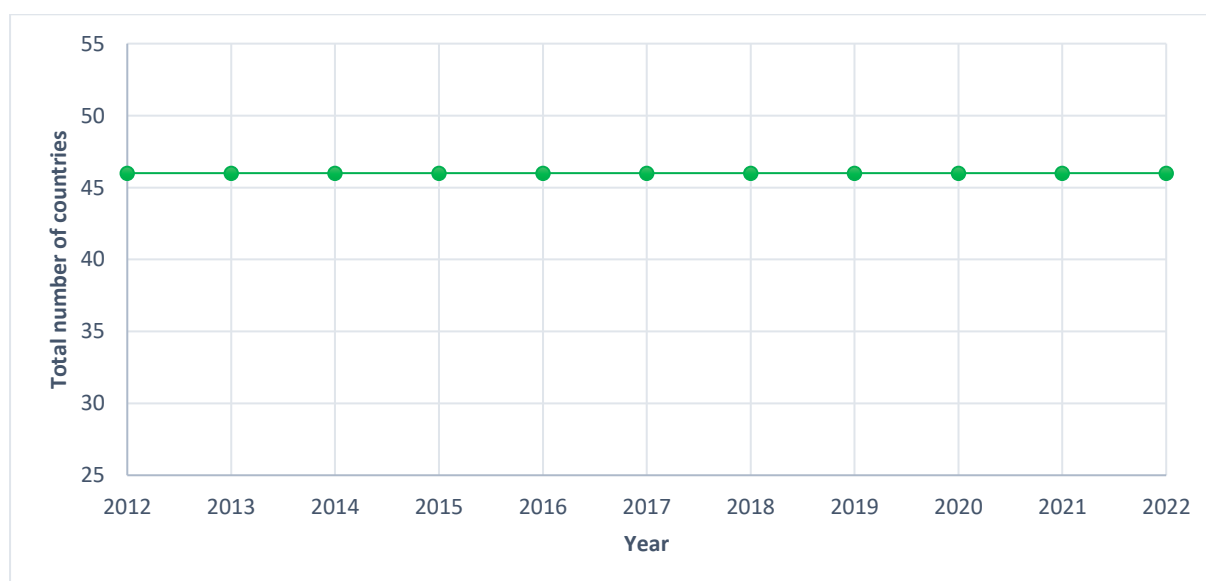


Figure 7.2 Development of national *ex situ* conservation systems.

The most common components of the *ex situ* conservation systems were storage facilities for seed, pollen and other tissue (reported by 45 countries), followed by *ex situ* conservation stands (44) and field collections (42 countries) (Figure 7.3). Eight countries reported other components (e.g. arboreta, botanic gardens and DNA banks) being included in their *ex situ* systems.

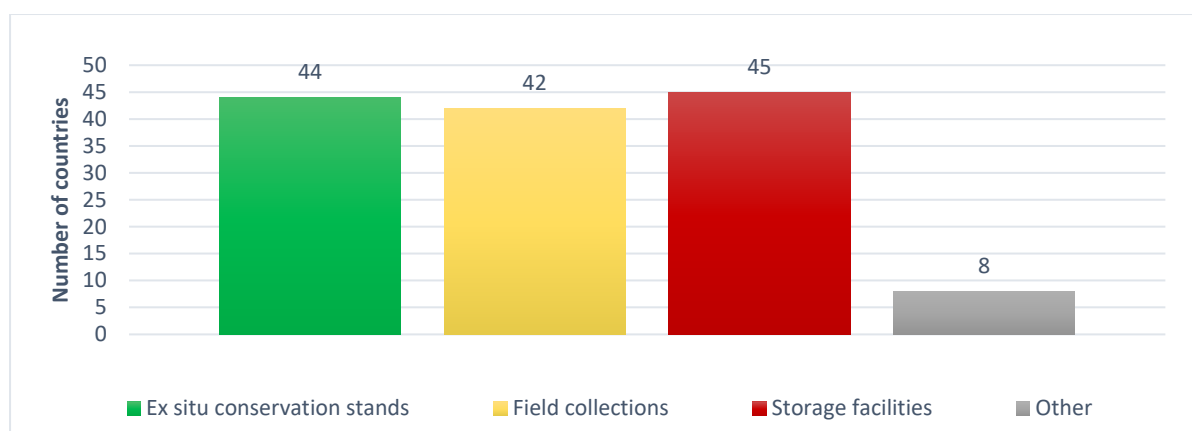


Figure 7.3 Different components of national *ex situ* conservation systems.

For this report, the countries reported 12 300 *ex situ* conservation stands covering nearly 165 000 hectares. Furthermore, 168 140 accessions in seed banks and field collections were reported globally. The reported *ex situ* conservation programmes include 978 species which represent less than 2 percent of the world's tree and other woody species. The number of species in these programmes was highest in Asia (403), followed by North America (202), and Latin America and the Caribbean (196) (Table 7.2).

The number of species under *ex situ* conservation reported here is considerably lower than what other global assessments have reported. For example, the GlobalTree Portal²² indicates that 17 825 (31%) of the world's tree species are found in *ex situ* collections (botanic gardens, arboreta and seed banks). The discrepancy is partly explained by the low number of countries (66), which provided data for the present assessment. It is also likely that the countries focused in their reporting only to those species, which are important for the forest sector and used in the forestry context (including agroforestry). Moreover, it is possible that *ex situ* conservation efforts documented by various agencies and other stakeholders remain scattered at national level and thus their information systems do not provide a comprehensive picture of all efforts made in this regard.

Table 7.2 Number of species, by regions, included in *ex situ* conservation programmes.

Region	Number of species*
Africa	138
Asia	403
Europe	159
Latin America and the Caribbean	196
Near East	1
North America	202
Southwest Pacific	52

* Net number of species reported by region

7.4 Conclusions

Tree genetic resources are in increasingly high demand due to the global forest and landscape restoration agenda, yet over the last decade the advances that have been made in *ex situ* conservation to support this agenda have been limited. Some progress has been made in modelling the storage

²² <https://www.bgci.org/resources/bgci-databases/globaltree-portal/>

characteristics and requirements for diverse sets of tree species, and potential exists for transcriptomic, proteomic and related approaches to provide further insights, but far more work is required to define the technical requirements of different germplasm storage methods. Most crucially, actions need to be taken to integrate the *ex situ* conservation of forest genetic resource into the actual practical implementation of tree planting, especially for native tree species. Models have in the last decade been refined to support this direction to action, including through the use of appropriately managed BSOs that can fulfil multiple functions simultaneously, albeit with trade-offs. But these models need to be scaled up and out from where they are currently applied. More innovative approaches to support conservation with growers – somewhere on the spectrum between *ex situ* and *circa situm* conservation – are required. This might, for example, involve the use of smartphone apps that allow farmers who have planted trees of conservation value to provide trees' proof of presence on their land, which could be linked to the digital payment of credits for their maintenance. Finally, it is necessary to better document the *ex situ* conservation of forest genetic resources at national level and make available comprehensive information on these efforts and the species included in the *ex situ* conservation programmes.

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**PART 4: STATE OF USE, DEVELOPMENT AND MANAGEMENT OF
FOREST GENETIC RESOURCES CONSERVATION**

CHAPTER 8. THE STATE OF USE OF FOREST GENETIC RESOURCES

8.1. Introduction

People have used the genetic resources of forest trees and other woody plant species for millennia to obtain wood and non-wood forest products. The use of these species for social, cultural, medicinal and scientific purposes also has a long history (Tegel *et al.*, 2012; Primavera and Fiorentino, 2013), and both forests and woodlands continue to provide numerous environmental services (FAO, 2014). This chapter focuses on the use of forest genetic resources for establishing new forests and tree-based production systems, and the subsequent chapters deal with the uses in the context of tree improvement and breeding (Chapter 9) and the management of existing forests (Chapter 10).

Seed is the most common form of tree germplasm used for raising planting stock but other plant parts (e.g. cuttings, buds, scions, explants and embryos) are also used for this purpose. The term *forest reproductive material* encompasses seeds and other plant parts, as well as plants raised by means of these parts (also including seedlings from natural regeneration) (OECD, 2022). Many trees have orthodox seeds (i.e. seeds that maintain their viability when dried and stored at low temperature) making it rather straightforward to collect and store seeds and then use them for establishing new forests and tree-based production systems. However, there is a considerable number of tree species, which have recalcitrant or intermediate seed. Such seed lack dormancy and are sensitive to both desiccation and low temperatures. This creates challenges for raising planting stock especially in humid tropics, where more than 70 percent of tree species have recalcitrant or intermediate seed behaviour (Sacande *et al.*, 2004).

Forest genetic resources have been increasingly transferred within and outside of species' natural distribution ranges during the past two centuries for growing trees for different purposes (Koskela *et al.*, 2014). Provenance research showed early on that the geographical origin of a seed source has a major influence on the growth and performance of planted trees (see König (2005) and references therein). Since the early nineteenth century, the guiding forestry principle for using tree species and their provenances has been the matching of climatic and other environmental conditions between a seed source and a deployment site.

During the past two or three decades, climate change has been increasingly posing great challenges for the above-mentioned principle as the climatic conditions in a given site have become a moving target with full of uncertainties for short- and long-term future (Harris *et al.*, 2006). To deal with an environment that is changing fast, and fast mean exceeding by far the pace for which adaptive mechanisms have evolved for millenniums, is a core element that must be incorporated in daily decisions for the management of forest genetic resources. This chapter will also discuss the speed of change of climate as a central environmental component to be considered, since other components of the environment, such as soil and topography, change naturally over a much longer period of time.

The Intergovernmental Panel for Climatic Change (IPCC) has reported that the increase in global surface temperature is of 1.09 °C (average for the period 2011-2020) above the pre-industrial reference period 1850–1900 (IPCC, 2022). There is more than 50% likelihood that global warming will reach or exceed 1.5°C in the near-term, even under very low greenhouse gas emissions scenarios, which would cause unavoidable increases in multiple climate hazards and present multiple risks to ecosystems (IPCC, 2022). There are already observed increases in the frequency and intensity of weather extremes on land. This has led to an increased drought-related tree mortality (Hammond *et al.*, 2022) and larger areas burned by wildfires in some regions (Jain *et al.*, 2022). Projected climate change, combined with non-climatic drivers, is expected to cause loss and degradation of much of the world's forests, as well as loss of biodiversity. For example, 3 to 14 percent of species assessed in terrestrial ecosystems are likely to face a very high risk of extinction at global warming levels of 1.5°C, increasing up to 3 to 18 percent at 2°C, 3 to 29 percent at 3°C, 3 to 39 percent at 4°C, and 3 to 48 percent at 5°C (IPCC, 2022).

8.2. Identification and selection of forest reproductive material

For many decades, forest and biology scientists, professionals and technicians have taken decisions on the identification and selection of forest reproductive material to be used based on the following general considerations:

- (1) The forest trees of interest are selected based on the main objectives of the management of natural or planted forests, for example the production of wood or fuelwood, or non-wood forest products. This selection is usually made based on historic experience, local biodiversity, access to natural stands, possibility to introduce species and results of species trials.
- (2) The best provenance that could grow healthy and deliver the best yield on a given deployment site is selected. This is typically done based on the results of provenance tests, which ideally cover the geographic distribution of a species (König, 2005).
- (3) The selection of mother trees with desirable phenotypes (typically good growth rate, straight stem and healthy) in natural stands or plantations, or good genotypes when progeny test results are available. The selection of mother trees could also be done in seed stands, seed areas (natural stands with a low intensity of selection of phenotypes), and sexual or asexual seed orchards (conformed by genotypes that have proven its genetic superiority in progeny tests, as part of tree breeding programs) (Zobel and Talbert, 1984). The selection could be done with very low intensity of selection, for example when silvicultural thinning operations remove first trees with less desirable phenotypes, and remaining trees at the last thinning might serve as seed trees. Seed collection for ecological restoration or genetic conservation programmes could prefer random selection of trees as seed source, aiming to encompass the maximum natural genetic diversity of the tree populations.

During this selection process (species of interest, best provenances and then best mother trees), it has been assumed that the climate, as main component of the environment where the next tree generations will grow, is stable, and that the historical average temperatures and precipitation are known, as well as the approximate extreme weather events that might occur.

This classical way to match the selected provenances with the environment is now insufficient. The environment has become a “moving target” because of climatic change (Harris *et al.*, 2006). Therefore, the major challenge is to match a contemporary provenance with a climate that is likely to occur on the deployment site in the future, i.e. after several decades. Moreover, the selected provenance should still be able to grow under today’s climate.

Climate change is expected to cause a steady increase of temperature, currently estimated to be about 0.27 °C per decade in continental areas globally (Hansen *et al.*, 2022). In addition, precipitation patterns are expected to become more variable and with lower precipitations in many regions of the world, in particular in those with continental climates. This will undoubtedly cause more severe episodes of drought increasing the mortality on forest ecosystems (Hammond *et al.*, 2022; IPCC 2022; Jain *et al.*, 2022).

Because of the above, it is likely that the interest in species and provenances that are more resistant to drought will grow, even at the cost of lower wood yield. Tree species that have so far been considered as “marginal” are expected to receive more attention, as well as the use of shrubs “nurse plants” providing shade to the target tree species). This can be illustrated with the following examples.

On the lower altitudinal (xeric) limit of *Pinus patula* (the fastest growing pine species of Mexico) at Sierra Norte of Oaxaca State, southern Mexico, the other pine species occurring is *Pinus oaxacana*, which have much slower growth rate than *P. patula*, but it is much more resistant to drought stress (Ruiz-Talonia *et al.*, 2014). It has been proposed that at its lower altitudinal (xeric) limit, *P. patula* should be planted with *P. oaxacana*. However, local forest owners so far dislike this idea because they (correctly) perceived that such species replacement would translate into lower wood yield per hectare in comparison with the planting of *P. patula* alone. Such positioning takes a short-term view, and does not consider the projections of the negative impacts of climatic change on *P. patula* stands at their xeric limit.

A similar example can be found from the lower altitudinal limit of *Pinus pseudostrobus*, another fast-growing pine species of the Purépecha Plateau in Michoacán State, central Mexico. At its lower altitude limit, *P. pseudostrobus* grows with *P. devoniana*, which is much more tolerant to drought stress due to its peculiar ability to delay its shoot elongation in spring, apparently to avoid the end of the warm and dry season between March and May (Castellanos-Acuña *et al.*, 2022). However, that mechanism and the fact that *P. devoniana* has a grass stage, means that it has a slower growth rate than *P. pseudostrobus*. Thus, *P. devoniana* would be the natural replacement at the low altitude of *P. pseudostrobus* (Sáenz-Romero *et al.*, 2012b), but forest owners are reluctant of changing species due to the lower growth rate of *P. devoniana* dislike.

8.3. Production of forest reproductive material

Seed stands, seed collection areas and seed orchards (clonal or sexual) have always been central to reforestation, tree breeding and commercial plantation programmes. The demand of seeds for seedling production in forest nurseries is expected to continue increasing, and also to shift towards new species. This results from the increasing efforts to restore degraded ecosystems and to use native or endemic species that have not been used commercially in the past (Commonwealth of Australia, 2019; Hoepfner and Hughes, 2019; Ruiz-Talonia *et al.*, 2022). It is also expected that the increasing mortality and declination of forests linked to drought events (Hammond *et al.*, 2022) will increase the demand of seedlings for reforestation.

Massive seedling production in forest nurseries of species for which there are not past experiences will impose the challenge of developing knowledge about the timing of seed collection, seed storage conditions and pre-germination treatments (Ruiz-Talonia *et al.*, 2022). Forest trees from harsh environments (long dry seasons, for example) have typically pronounced mechanisms of seed dormancy to prevent germination outside of the appropriate (i.e. rainy) season.

In Mexico, for example, climate change will decrease suitable climatic habitat for pine forests, and increase the habitat suitable for dryer forests (Rehfeldt *et al.*, 2012; Gómez-Pineda *et al.*, 2020), such as the one dominated by oaks and legume trees. Since Mexico is the centre of diversity for oaks (*Quercus*) (Nixon, 1993), this presents a challenge as the acorns are very difficult to store, there are not a culture of having seedling banks instead seed banks, and there is less knowledge about the biology of several species to transit to a massive production of seedlings in forest nurseries.

Seed stands and seed areas on the rear end of the species' distribution range would gradually experience a decrease of their seed production, given the expected increase of environmental stress due to heat waves and drought periods. Therefore, if those stands and areas contain remarkable genotypes, it would be necessary to conserve them *ex situ*, both at seed banks and *ex situ* stands on sites that will have a suitable climatic habitat for these genotypes in the future.

8.4. Certification of forest reproductive material

Certification of forest reproductive material, i.e. providing reliable information on species, place of origin (provenance), number of seeds per kilogram and germination rate, is essential for a fair trade of the material both domestically or internationally, as well as for the appropriate planning of seedling production on the nurseries and the use of the material. It is important to note that such certification does not guarantee the appropriate place of deployment, but based on the information provided, the buyer can decide where to use the material. Due to climate change, it is necessary adjust the current deployment zones of a given material and the use of local seed sources will become a less desirable option. In the future, the certification of forest reproductive material is becoming even more important for the use of forest genetic resources and those countries, which do not have yet such certification system in place, should consider creating one as soon as possible. Many countries have designed their certification system following the OECD Forest Seed and Plant Scheme (OECD, 2022) but they may

have not joined officially this scheme allowing certification of the material for international trade. In fact, only 29 countries have so far joined the OECD scheme although it is open to all countries.²³

Climate change is also likely to increase the international trade of forest reproductive material and thus the demand for certified material. In British Columbia (Canada), for example, 21 percent of seed zones are expected to be at moderate or high risk of lacking domestic provenances adapted to the climate projected for 2040, and such shortage has been proposed to be filled by seed sources from Pacific Northwest of USA (O'Neill and Gómez-Pineda, 2021).

8.5. Deployment of forest reproductive material

The deployment of forest reproductive material aims to maximize tree survival, growth and pest resistance by using appropriate material on a given site. Historically, seed has been collected within a deployment area with an aim to promote the use of local seed sources. However, “local” has been defined in various ways and some early guidelines limited transfer distances to 160 km and to 330 m of altitudinal difference between the seed collection and deployment sites (e.g. McCall, 1939). More elaborated deployment guidelines have been developed based on multiple seed zones and subzones along latitudinal, longitudinal, elevational and moisture gradients (e.g. Buck *et al.*, 1970; Millar and Libby, 1991), and presently these guidelines are increasingly refined based on climate change projections (e.g. O'Neill *et al.*, 2017).

In many tree species, climate change has already affected the current deployment areas. The challenge for forest managers is to match seed from the currently available sources with the present and future climates of deployment sites.

To understand how the deployment guidelines need to be modified, it is necessary to consider the expected impacts of climatic change on forest ecosystems and on forest genetic resources in particular, as well as the migration of forest tree populations by natural means.

8.5.1. Impacts of climatic change

Temperature increase is creating a serious stress on forest tree populations that is shown as defoliation and weakness of the trees, reduced growth, increased pest outbreaks and forest fires and even unusually large mortality trees worldwide (Allen *et al.*, 2010, 2015; Hammond *et al.*, 2022). Stressed trees are also producing less seeds and with less germination potential (Alfaro *et al.*, 2014; López-Toledo *et al.*, 2017).

The most vulnerable tree populations are those located on the xeric limit of a given tree species' natural distribution range. Typically, the upper altitudinal or northern limit (in the Northern Hemisphere), or the southern limit (in the Southern Hemisphere), of a tree species is defined by cold temperatures. The other extreme, at the lower altitudinal limit or southern limit (in the Northern Hemisphere) or the northern limit (in the Southern Hemisphere), is defined by drought stress, also called the xeric limit (*sensu* Mátyás, 2010). Tree populations located in the xeric limit have historically suffered periodic drought stress. However, what is happening with climate change is that the phenotypic plasticity that has permitted to these tree populations cope with droughts is exhausting because their growing sites are becoming even dryer and warmer. Since trees cannot “walk”, they can only migrate very slowly mechanisms through seed dispersion, followed by the successful establishment of propagules and competition, before reaching the sexual maturity to repeat the process again. It has been reported that adult trees simply cannot stand the new hotter and dryer conditions, and that they are dying along the contemporary xeric limits (Mátyás, 2010; Mátyás *et al.*, 2010).

In different parts of the world, ecological niche models applied for contemporary biomes (types of vegetation) or forest trees indicate shifts, and often even net reductions, in distribution ranges because of climate change. In North America (from Honduras to Alaska), the models indicate a reduction of

²³ <https://www.oecd.org/agriculture/forest/>

the climatic habitats suitable for biomes associated to moist and cold climates, and an expansion of the habitat suitable for biomes associated to dryer and warmer climates (Rehfeldt *et al.*, 2012). In Europe, the reduction of suitable climatic habitat is projected for one of the most important oak species, *Quercus petraea*, which is expected to lose habitats in particular on the south-eastern limits of its current distribution in Hungary and Türkiye (Sáenz-Romero *et al.*, 2017). In Eurasia, a significant reduction of the contemporary distribution, and its shift toward north-east, has been projected to *Pinus sylvestris* and *Larix sibirica*, two of the most important tree species (Tchebakova *et al.*, 2005).

It is important to note that when the ecological niche models predict reductions in a suitable climatic habitat, this does not necessarily mean that a species will disappear from certain areas. However, when the models predict disappearance of the suitable climate, the existing trees are likely to be exposed to a severe stress. Similarly, if the models project a habitat expansion, this does not necessarily mean that tree species are actually able to expand their distribution range. Therefore, these models should be used only as a tool to evaluate the likely impacts of climate change, and to allow forest managers to take informed decisions.

8.5.2. Speed of natural migration

There is evidence that tree species are already migrating naturally in response to climate change. For example, *Quercus ilex*, an oak able to grow in drier and warmer sites than other European oaks, is expanding in the northern margin of its historical distribution on sites that were too cold and moist in the past for it to compete successfully with other species present (Delzon *et al.*, 2013).

In addition to extending distribution at their range margins, climate change can also affect the spatial core of the distribution range of trees. Lenoir *et al.* (2008) showed that climate change had resulted in a significant upward shift, averaging 29 meters per decade, in the altitudinal distribution of 171 forest plant species in the French Alps. The same authors also reported that, due to their ecological and life history traits, trees and shrubs were two to three times slower than other species (herbs, ferns and mosses) in shifting their optimum elevation upward. This raises a question whether the speed of natural migration in trees is fast enough to follow the suitable climate habitat.

In the Pyrenees Mountains of Spain, the timberline of *Fagus sylvatica* has also been recorded shifting upward approximately 43 meters of elevation during the past 80 years while average temperature has increased by 1.5 °C in the area (Peñuelas *et al.*, 2007). However, such temperature increase has shifted suitable conditions for the species upwards by 200-300 meters in altitude so the results of Peñuelas *et al.* (2007) suggest that the speed of natural migration was much slower than the speed of changing climatic conditions. The speed of natural migration also seems slow in less mountainous areas. In the United States of America, Ash *et al.* (2017) compared the northwards shifts of the natural range centroid of 78 forest-understory plant species- in Wisconsin between 1950 and 2000 to the corresponding shifts in climate and found that the species have shifted in average 49 kilometres northwards, meanwhile the climate has shifted 114 kilometres (Ash *et al.*, 2017). In this case, the vegetation shifted less than half of the speed of the suitable climate conditions.

8.5.3. Population-level responses to climate change

The projected reduction and shifting of location of the suitable climatic habitat of a forest tree species indicate the dangerous expected impact of climatic change on the forest genetic resources. However, even if there were not a net reduction of the suitable climatic habitat, and there were only a shifting of place of the suitable climatic habitat, there will be a pernicious effect. That is because

Forest tree populations differentiate genetically along environmental gradients demonstrating their adaptation to the environment in which they grow (Rehfeldt, 1988; 1999b). In other words, although a species can appear being adapted to a relatively large geographical area, the individual populations of a given species are actually adapted to a narrower range of environmental conditions.

This population-level of differentiation can be measured when growing provenances of forest trees originating from different climates in common gardens (see also Chapter 5). Associating the average expression of quantitative traits per provenance, such as height growth, resistance to frost damage or biomass growth, it is possible to estimate, for example, how much difference in altitude of seed source makes two populations statistically different for the genetically controlled expression of those quantitative traits (Rehfeldt *et al.*, 2018). It has been shown, for example, that two populations are genetically differentiated when they are separated by an altitudinal difference of 240 meters in *Pseudotsuga menziesii*, 300 meters in *Pinus contorta*, 420 meters in *Picea engelmannii*, and 450 meters in *Pinus albicaulis* (Rehfeldt *et al.*, 2020). Other studies have reported an altitudinal difference of 200 meters for *Pinus oocarpa* (Sáenz-Romero *et al.*, 2006) and for *P. patula* (Ruiz-Talonia *et al.*, 2014), 300 meters for *P. pseudostrobus* (Sáenz-Romero *et al.*, 2012b), 350 meters for *Abies religiosa* (Ortiz-Bibian *et al.*, 2017), and 400 meters for *P. devoniana* (Sáenz-Romero and Tapia-Olivares, 2008). All these altitudinal difference values can be translated into climatic variables since altitude is actually a surrogate variable for climate clines.

The average of the above-listed altitudinal differences making two tree populations significantly different is 318 meters. This value is equivalent to about 1.5 °C, a relatively narrow part of the climatic space occupied of any of the forest tree species listed. Such value is extremely important, because it illustrates that even if there is not a net reduction of the suitable climatic habitat for a given species, a shift of place (for example, a displacement northwards or to higher altitudes) will decouple the individual populations from the narrow interval of suitable climate for which the populations have adapted to. It is also important to keep in mind that such narrow adaptive climatic interval of 1.5 °C will be exceeded within the current decade as a result of climate change.

8.5.4. What are the options for adaptive management?

Considering the magnitude and speed of climate change and the rather slow speed of natural migration in forest trees, as well as the fact that individual populations of forest trees are adapted to a rather narrow climatic interval, it can be asked to what extent management interventions are needed to support the adaptation of forest tree populations to climate change.

One option is to do no management and put faith in natural selection to act on the existing genetic diversity within populations and to select genotypes able to survive under new climatic conditions. This would be a dangerous option as it ignores that forest decline is already happening in many regions of the world. It is also unclear if phenotypic plasticity and the existing genetic diversity of tree populations can ensure their adaptation to the fast pace of climate change, especially at the xeric limit of tree species' distributions.

Moreover, trees might be able to survive droughts, heat waves and pest attacks, but become so weakened that they practically stop producing seeds (López-Toledo *et al.*, 2017). Should this happen, the management options, including conservation efforts, would be very limited.

Alternative options involve different degree of management interventions and these have been labelled as assisted migration, assisted colonization, assisted relocation or facilitated migration (Rehfeldt *et al.*, 2002; Aitken *et al.*, 2008; Hewitt *et al.*, 2011; Pedlar *et al.*, 2012; Tchebakova *et al.*, 2005; Dumroese *et al.*, 2015).

In general, the deployment areas of seed and seedlings could be adjusted based on the observed and projected changes in climatic conditions. The main objective is to have healthy trees well adapted to the present and future conditions on a given site, so that they are able to produce the next tree generation that can survive and mature under future conditions. Assisted migration challenges a fundamental concept of classical restoration ecology and many existing silvicultural practices, i.e. that local seed sources are normally the best, or at least among the best ones. However, the results of provenance trials with many forest trees have shown that "local" provenances are not consistently the best ones (see below) and climate change is making the concept even more problematic (e.g. Ledig and Kitzmiller, 1992; Sáenz-Romero *et al.* 2016).

For assisted migration, it would be wise to choose a climate transfer distance that considers a time period that accounts for the climate change that has already taken place, plus a portion of the rotation age of a given tree species (considering that early ages are the most vulnerable in a tree's life cycle) under a projected climate scenario. For example, British Columbia's new Climate Based Seed Transfer (CBST) system recommends migrating seed a climate distance equivalent to the amount the climate has changed since a normalized reference period (1931-1960 in their case), plus the expected climate change during the following 15 years (i.e., ¼ rotation) after planting. In this example, 15 years after planting, tree populations would be growing under the climate in which they existed prior to the onset of anthropogenic climate change (O'Neill *et al.*, 2017). As the rotation age varies among species, the targeted future climate time period would be different for each managed species.

The shifting of provenance selection towards colder and moister sites, to compensate the ongoing and future climate change, would imply different types of movement in respect to the contemporary species distribution (Dumroese *et al.*, 2015; Ipinza and Müller-Using, 2021; Sáenz-Romero *et al.*, 2021):

- Shifting the provenances within the contemporary natural distribution range of a species (for example, from a lower altitude to a higher altitude inside the elevational gradient of the current natural distribution).
- Shifting the provenances outside the current natural range of a species, near its upper altitudinal, northern or southern cold limit. This has been called species' range expansion. For example, shifting provenances polewards, like the transfer of *Pinus albicaulis* northwards beyond its current north limit in British Columbia, or at higher altitudes beyond the contemporary timber line (McLane and Aitken, 2012), or in the case of *Araucaria araucana*, towards southern Chilean locations (Ipinza and Müller-Using, 2021; Ipinza-Carmona *et al.*, 2022). Another example is to transfer to another mountain of higher altitude, when the summit puts a limit than need to be exceeded. This is the case of *Abies religiosa* in the Monarch Butterfly Biosphere Reserve in Mexico, where summits are about 3 550 meters of altitudes, coinciding the upper altitudinal limit of the species that needs to be expanded at least 300 meters in altitude to compensate 1.5 °C of warming (Sáenz-Romero *et al.* 2012a; Carbajal-Navarro *et al.*, 2019).
- Shifting provenances to extreme far away sites, when there is no projected future suitable climatic habitat near of the contemporary distribution. This might be needed for rare, endemic, endangered or glacial relict species of very limited and fragmented populations, like yew-like conifer *Torreya taxifolia*. Its natural distribution is extremely reduced (about 1 000 individuals) in Florida, and they would need to be translocated about 500 kilometres northwards (McLachlan *et al.*, 2007; Barlow, 2011). Other extreme example is endangered *Picea mexicana*, that would need a trans-continental transfer from its only three remaining populations in northern Mexico to the Himalayas, for example (Mendoza-Maya *et al.*, 2022).

8.5.5. Resistance to assisted migration

The acceptance of assisted migration among forest managers, conservationists and public vary depending on the geographical distance of a proposed provenance transfer. The provenance transfers within the natural distribution ranges of species are generally accepted but are considered controversial and highly controversial in the cases of the species range expansion and the far away translocation, respectively (Peterson St-Laurent *et al.*, 2019).

Since the transferring of provenances within the natural distribution ranges of tree species is already a customary forestry practice (albeit done historically to increase wood production, rather than as a response to climate change), assisted migration seems to be generally more accepted among forest managers. Conservationists, who consider no, or minimum, human intervention as the best way to let natural forces act to conserve the ecosystems, perceive assisted migration as a too extreme human intervention, and therefore, undesirable.

There can also be other reasons for objecting assisted migration. These include short-term economic interests, for example when the migrated species have slower growth rate as compared to the existing species (see the example of *Pinus pseudostrobus* and *P. devoniana* on Section 8.2). They can also be rules or even laws prohibiting the transfer of species or its provenances to protected areas where it is not endemic, even when assisted migration might save an endangered species from extinction (this is the case of *Picea mexicana* (Ledig *et al.*, 2010; Mendoza-Maya *et al.*, 2022)).

It is likely that the debate on assisted migration will continue and that the positions may change, especially when climate change and other drivers are expected to increase the number of species extinctions (Brook *et al.*, 2008).

8.5.6. Lessons learnt from provenance tests

One way to contribute objectively to the debate on assisted migration is to consider the results of field experiments, which are actually experimental deployments of provenances either to colder and moister sites, or to warmer and dryer sites, to evaluate the potential impacts of climate change. For this purpose, climatic transfer functions have proven extremely useful.

Campbell (1974), followed by Mátyás (1994), Schmidting (1994), Rehfeldt (1999a, 1999b) and others, envisioned the utility of revisiting old provenance tests of forest trees as a source of information to predict the performance of provenances on a site with a different climate as compared to the seed source. By the early 1990s, this was not only done for identifying best-yielding provenances but also for studying possible impacts of climate change, and for developing alternative forest management guidelines to accommodate such impacts. A new concept, the climatic transfer distance, was proposed to describe the difference between the climate of the planting site and that of the seed source, named initially “ecological transfer distance” or “ecodistance” (Mátyás, 1994). Average survival and growth per provenance could then be examined as response variables to the climatic transfer distance (Mátyás 1994; Schmidting 1994; Rehfeldt 1999a, 1999b). This was a critical step for moving forward from what was a relatively simple way of choosing the best provenance in terms of yield, towards a better comprehension of *why* a provenance might be better than others on a given planting site. Such conceptual development opened a new field known today as genecology, an overlapping field between population genetics and population ecology.

The analysis of the provenance response to a climatic transfer distance is frequently expressed as a response function with a quadratic curve. The best performance is on or close to the seed origin (where transfer distance is zero or very small), and the decay increases with the climatic transfer distance, either towards colder and more moist sites, or towards warmer and dryer sites. These models have become more sophisticated and benefitted from the arrival of complex statistical mixed models, that among other features split the genetic differences among provenances in more than one source of variation. These include the effect of climate on a provenance (a fixed effect that accounts for population genetic differentiation due to the selection pressure of climate at the provenance site), and other within-populations genetic effects. Detailed explanations of these models can be found in Wang *et al.* (2010) and Leites *et al.* (2012a; 2012b).

Provenance tests provide a wealth of information that is helpful for addressing climate change questions. However, few provenance tests older than 20 years are located in climates or locations outside the natural climatic or geographic distribution of the species. In fact, older provenance tests were often placed on good quality sites, well inside the species distribution range, where it was expected the species would be most frequently planted (Illingworth, 1978). Placing provenance tests on marginal sites was considered a waste of resources. However, the need for tests sites outside species' natural distributions and wide-ranging transfers to ‘tie-down’ the tails of transfer and response functions are now widely acknowledged (Leites, 2012b; O’Neill *et al.*, 2014). Furthermore, old provenances tests have frequently blurred the genetic differences among provenances by the long-term effects of other factors than climate, such as competition, insect and pest attacks and loss of labels.

For the above reasons, provenance tests designed *ex professo* and located at sites beyond the cold limit of species' current distributions are urgently needed to test the feasibility of assisted migration. Likewise, provenance tests located at sites beyond the warm or dry (xeric) limit of species' current distributions are also needed to assess impacts of climate change. Examples of large trials designed explicitly to respond questions related to climate change, where each species have some testing sites outside its current climatic and geographic range, are the Assisted Migration Adaptation Trial (AMAT, 47 populations from 15 species planted at 48 test sites across western North America) (Marris 2009), the interior spruce genecology/climate change trial (128 populations of *Picea engelmannii* X *glauca* tested at 17 sites in British Columbia, Alberta and Yukon) (O'Neill *et al.* 2014), and REINFORCE (150 populations from 38 species tested at 41 locations in western Europe).

The following examples provides some lessons learnt from selected provenance tests analysed with climatic transfer functions to evaluate the climate change impacts for the management of forest genetic resources.

In case of Chinese tree species *Platycladus orientalis*, tested with 69 provenances at 19 common garden experimental sites, non-local provenances transferred to northern and northwestern China outperformed local ones in peripheral areas, suggesting an adaptational lag in these areas (Hu *et al.*, 2019). Projected tree height of this species would decline by 4%–8% if local provenances were used. Thus, assisted migration with properly selected seed sources would be effective in avoiding maladaptation in new plantations under a changing climate (Hu *et al.*, 2019).

Six European tree species (*Abies alba*, *Fagus sylvatica*, *Quercus petraea*, *Pinus pinaster*, *Pinus pinea* and *Pinus nigra*) were tested with 706 populations on 97 common garden experiments. The results indicate adaptation lags consistently higher in climatic margin populations (cold/warm and dry/wet). Predictions for future warmer climates suggest adaptation lags would decrease in cold margin populations, slightly increasing tree height, while adaptation lags would increase in core and warm margin populations, sharply decreasing tree height (Fréjaville *et al.*, 2020). An expected severe reduction of growth and survival for *Q. petraea* at its extreme southeaster margin of the natural European distribution (Hungary and Turkey) was confirmed by Sáenz-Romero *et al.* (2017) and Mátyás (2021).

When re-examining multiple long-term provenance tests of four tree species in Europe and Eurasia, deciduous broadleaf species (*Quercus petraea* and *Fagus sylvatica*), exhibited flatter function curves as growth response to climatic transfer distances, indicating more phenotypic plasticity and less among population differentiation along climatic gradients, than conifers species (*Picea abies* and *Pinus sylvestris*) (Sáenz-Romero *et al.*, 2019). These results for *F. sylvatica* (large plasticity and low climatic sensitivity) were confirmed by Gárate-Escamilla *et al.* (2019). This suggests that perhaps conifers will be more impacted by climatic change than deciduous broadleaved species.

The analysis of tree height and survival of 313 populations of *Pinus sylvestris* planted on 36 sites, and of 130 populations of *Larix* ssp. (63 of *L. sibirica*, 42 of *L. gmelinii*, and 25 of *L. sukaczewii*) planted on 8 sites, indicated that seed sources, grouped as “climatypes”, could be transferred to the expected future location of their climatic optima, involving geographical distances of 700–1200 kilometers for these species (Rehfeldt *et al.*, 2003; Tchebakova *et al.*, 2005).

An analysis of extreme provenances and tests sites from southern margin (Spain) and northern margin (Nordic countries) of *Pinus sylvestris*, indicated that tree height adaptation is mostly driven by drought in Spain and by photoperiod in the Nordic countries (Hallingbäck *et al.*, 2021).

A very long-term *Pseudotsuga menziesii* progeny and provenance tests (planted in 1912) in multiple sites in Oregon and Washington State (120 parents, 13 seed sources, 5 field sites), indicated that it is safe (in terms of an acceptable loss of growth and survival) to transfer provenances towards colder sites (to compensate climatic change) of a magnitude of 2 °C to 3 °C of climatic transfer distance (StClaire *et al.*, 2020).

An evaluation of multiple provenance trials of five most important eastern North American tree species (*Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Pinus strobus* and *Betula alleghaniensis*) indicated that optimal height growth at test sites can be achieved with a modest warm-to-cold (generally northwards) seed transfers on average of 1.6°C. However, much larger critical seed transfer distances can be done to reach more than 90 % of optimal height growth (Pedlar *et al.*, 2021). The need to transfer northwards for *P. strobus* was also confirmed by Joyce and Rehfeldt (2013).

A reciprocal common garden tests along an altitudinal gradient in Mexico indicated that for every 100 m of transferring a *Pinus pseudostrobus* seed source upward in altitude, there is a loss of 5 % in growth (Castellanos-Acuña *et al.*, 2015). It has also been found acceptable, in terms of growth and survival, to transfer *Abies religiosa* provenances upwards up to 400 meters in altitude in the Monarch Butterfly Biosphere Reserve in Mexico, under the conditions that *A. religiosa* seedlings would be planted under the protective shade of existing shrubs (e.g. *Baccharis conferta*) (Carbajal-Navarro *et al.*, 2019).

[8.6. State of the use based on country reports]

[8.7. Conclusions]

8.9. References

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[CHAPTER 9. THE STATE OF GENETIC IMPROVEMENT AND BREEDING PROGRAMMES]

[CHAPTER 10. MANAGEMENT OF FOREST GENETIC RESOURCES]

PART 5: STATE OF CAPACITIES AND POLICES

CHAPTER 11. INSTITUTIONAL FRAMEWORK FOR THE CONSERVATION, USE AND DEVELOPMENT OF FOREST GENETIC RESOURCES

11.1. Introduction

The first-ever State of the World's Forest Genetic Resources (FAO, 2014a) and the Global Plan of Action (FAO, 2014b) called for strengthening countries' commitment to create an enabling institutional environment for FGR conservation, use and development at national or subnational levels. This chapter presents the status of the institutional framework for FGR, based on the reported national coordination mechanisms, national strategies for FGR, mainstreaming FGR into relevant national policies, and capacity building on FGR. The broad range of national institutional frameworks reported by the countries highlights the cross-sectoral nature of FGR and reflects the institutional complexity associated with environmental governance also reported by earlier studies (e.g. Rodríguez Fernández-Blanco, Burns and Giessen, 2019; Zelli, Nielsen and Dubber, 2019; Engels and Rudebjer, 2017; Rayner, Buck and Katila, 2010). The findings of the present report also highlight the need to take into consideration the national institutional context and all relevant stakeholders, as well as needs and priorities for strengthening national institutional frameworks on FGR.

11.2. National coordination mechanisms on FGR

A national coordination mechanism encompasses a range of approaches to coordinate the work on FGR at national and/or subnational levels and serves as a point of convergence for stakeholders to coordinate existing and new activities within the forest sector and with other sectors. Examples of stakeholders involved in the conservation, use and development of FGR include farmers, forest owners, private sector, NGOs, governmental organisations (including state-owned enterprises), research organisations (including universities), and relevant ministries. A national coordination mechanism may take the shape of a national committee, working group or programme on FGR, depending on country-specific priorities, needs and capacities (FAO, 2023).

The Global Plan of Action stressed the need for coordination of the work on FGR at national level as "knowledge on FGR is usually scattered and held by various institutions" (FAO, 2014b). It also urged to promote national coordination, including collaboration between institutions and programmes, and the creation of national consultation frameworks based on willing and inclusive participation of all relevant stakeholders (FAO, 2014b).

For the present report, 38 countries reported having a national coordination mechanism on FGR in place and 10 countries reported having initiated the establishment of such a mechanism (Figure 11.1). In 2012, at least 28 countries had established a national coordination mechanism on FGR (Figure 11.2). Between 2012 and 2020, eight countries (Ireland, the Islamic Republic of Iran, Japan, Luxembourg, Malta, Mexico, the Russian Federation and South Africa) reported having established such a mechanism. No new national coordination mechanisms have been established since 2020 (Figure 11.2). Of the 38 countries with the national coordination mechanism, two were unable to report the establishment year.

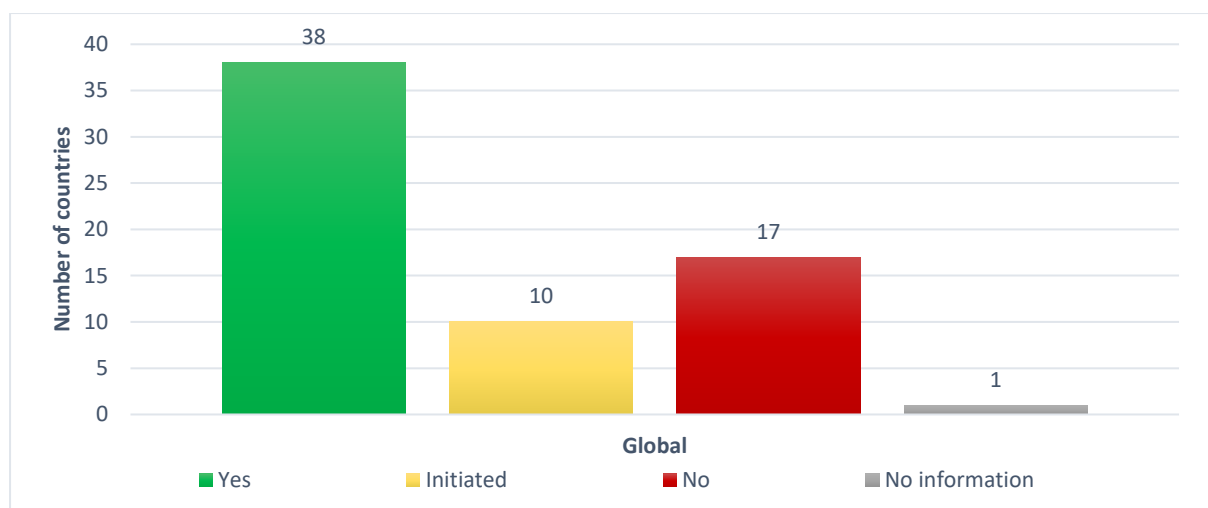


Figure 11.1 Number of countries with national coordination mechanisms on FGR

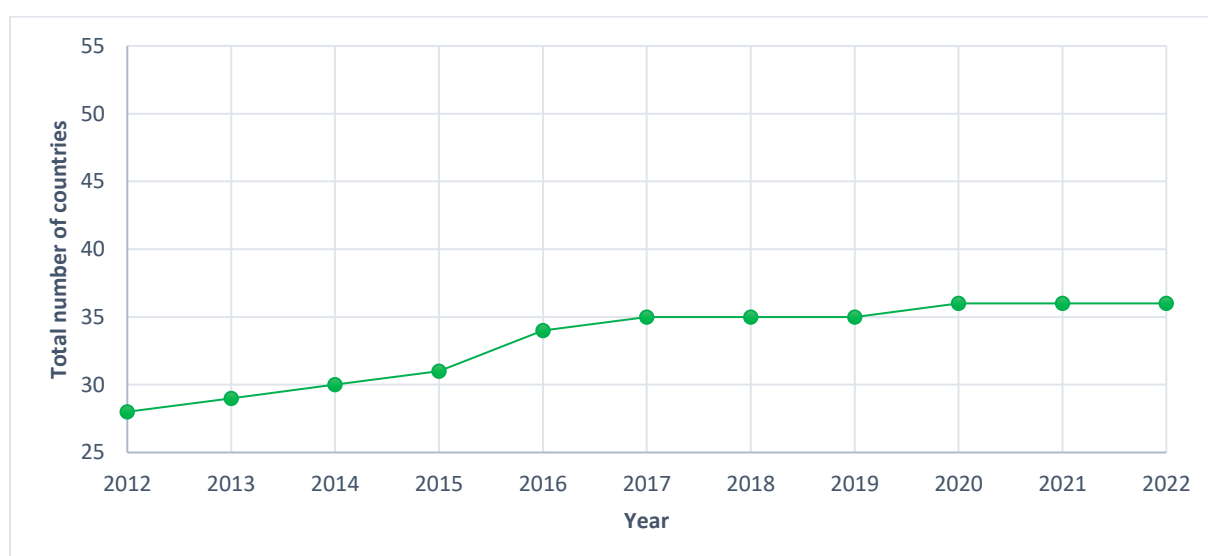


Figure 11.2 Development of national coordination mechanisms on FGR.

Most of the reported national coordination mechanisms engage multiple stakeholder groups, as recommended by the Global Plan of Action. The main stakeholders involved in the national coordination mechanisms are governmental organizations (reported by 38 countries) and research organizations (36), followed by relevant ministries (23), forest owners (17) and non-governmental organizations (NGOs) (17) (Figure 11.3). Less countries reported the involvement of the private sector (15), farmers (7) and other stakeholders (2)

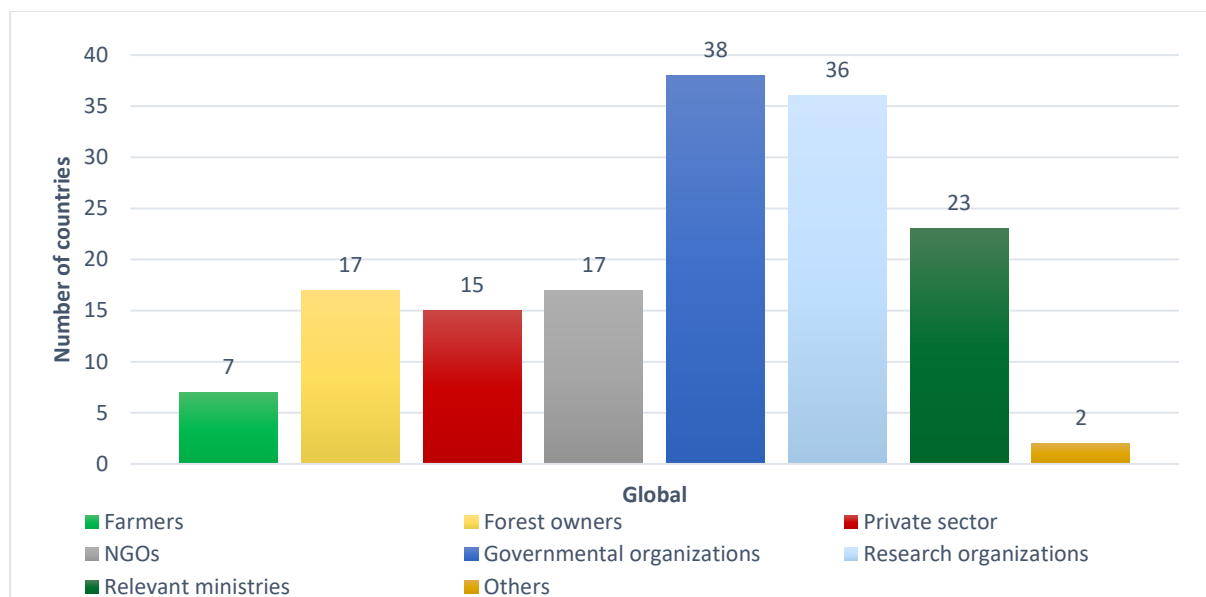


Figure 11.3 Stakeholders involved in national FGR coordination mechanisms.

The first national coordination mechanisms reported date back more than 50 years (e.g. in Czechia, Iceland, Thailand and Ukraine). Concerning stakeholders, countries reported a range of different ministries having the mandate on forests and budget allocations for FGR conservation, use and development, such as the Ministries of Environment, Agriculture, Fisheries and Forests, Rural Development, Industry and Trade, and Natural Resources and Tourism. Governmental organizations with responsibilities related to FGR include state-owned forest enterprises (SOFEs), national seedbanks, national botanic gardens, and municipal and state forest agencies. Universities and forest research centers are examples of research organizations that conduct relevant R&D activities, such as forest seed testing, tree breeding, and genetic conservation prioritized tree species. As the management decisions of forest owners impact the conservation and use of FGR, these stakeholders are also engaged in national coordination efforts. Other FGR stakeholders include farmers, NGOs (e.g. conservation NGOs, farmers’ or foresters’ associations) and private sector (e.g. tree nurseries, forest industry).

In 2015, public ownership (e.g. by state, county or municipality) was the predominant category of forest ownership worldwide at 73 percent of the global forest area (FAO, 2020b). Private ownership (e.g. by individuals, enterprises, local communities and indigenous peoples) accounted 22 percent of the global forest area but in regions like Central America and Europe,²⁴ it is the dominant form of forest ownership (FAO, 2020b).

Countries have followed two main approaches in the establishment of a national coordination mechanism on FGR: a “stand-alone” mechanism to coordinate specifically the work on FGR, or an “integrated” approach as part of broader coordination efforts on FGR-related topics, such as forests or biodiversity. For example, Eswatini reported that the coordination of FGR, including the equitable sharing of benefits, is overseen by the National Environment Office and implemented under the second National Biodiversity Strategy and Action Plan (2016)²⁵ and the Access and Benefit-sharing guidelines. Eswatini describes the coordination of work on FGR as part of the biodiversity agenda as a “step towards establishing a mechanism that will be strictly for FGR” (Eswatini Country Report). Lithuania reported that it established a stand-alone National FGR Advisory Group in 2005 to provide “overall guidance and direction for FGR at national level”. Lithuania’s National FGR Advisory Group is chaired by the State Forest Service and the main stakeholder groups involved are governmental and research organisations (Lithuania Country Report). In Mexico, the coordination is organized by both a stand-alone Forest Genetic Resources Network involving public, private and research institutions, and

²⁴ Except the Russian Federation, where all forests were publicly owned in 2015

²⁵ <https://www.cbd.int/doc/world/sz/sz-nbsap-v2-en.pdf>

integrated coordination efforts on forests, biodiversity, protected areas and plant genetic resources led by national institutions CONABIO, CONANP, SINAREFI and others.

Countries that have not established a national coordination mechanism on FGR reported more “fragmented” coordination efforts targeting specific sectors and/or areas of work on a periodic and/or *ad hoc* basis, for instance in the context of protected area management or forest reproductive material. Examples of these countries include Chile, where FGR is managed through various parallel public and private sector initiatives, and Estonia, where FGR stakeholders (working on specific aspects of FGR) are consulted on relevant legislative and strategic processes as needed.

The first global assessment on FGR found that the coordination is often lacking and called for increased synergy and coordination between national institutions (FAO, 2014a). The findings of this second global assessment show that progress has been made in strengthening the national coordination on FGR and that 58 percent of the reporting countries had a national coordination mechanism in place. The findings further show that the national coordination mechanisms engaged multiple stakeholders, albeit often the participation is dominated by governmental and research organizations. The different approaches to national coordination of FGR that can be summarized as “stand-alone” (e.g. National Working Group on FGR), “integrated” (e.g. National Working Group on a broader topic including FGR priorities) and “fragmented” (e.g. *ad hoc* coordination involving specific stakeholders on specific areas of work). The approach preferred by a country depends on the national institutional context related to FGR and forests, as well as relevant stakeholders, processes and priorities.

11.3. National strategies for FGR and the integration of FGR into relevant national policies

The global assessment stressed the need for sound national policies and regulations on FGR, and integration of FGR into broader national policy frameworks to facilitate appropriate action (FAO, 2014a). Countries can follow different in the preparation of a national strategy on FGR, as well as various options for integrating FGR into relevant national policies (FAO, 2023). One of the key national policies is forest policy, which describes a country’s long-term goals for the development of the forest sector (FAO, 2010). It may be complemented by a strategy and an action plan to translate long-term policy goals into a specific, measurable and time-bound framework for action. Additionally, legislation may be developed to facilitate the implementation of a forest policy (FAO, 2010). The next sections present the state of national strategies for FGR, and integration of FGR into relevant national policies related to forests, biodiversity and climate change.

11.3.1. National strategies for FGR conservation, use and development

A national strategy for FGR is a document, which translates a country’s needs, priorities and vision related to FGR conservation, use and development into a concrete, actionable framework. The development of a national strategy on FGR is based on the national status of FGR, and ideally includes a description of the priorities, targets, actions and responsible stakeholders, as well as aspects related to resource mobilization and monitoring. A national strategy on FGR typically aligns with existing national or subnational forest policies and/or national forest programmes (NFPs), as well as international commitments such as the Convention on Biological Diversity (FAO, 2023).

The first global assessment found that relevant national policies and programmes often inadequately address FGR (FAO, 2014a), and the Global Plan of Action thus stressed the need for policy tools that provide a framework for action on FGR including the development of national strategies on FGR (FAO, 2014b).

For this second global assessment, 41 countries reported having a national strategy (or subnational

strategy) for FGR conservation and use in place, and 12 countries reported having initiated the establishment of such a strategy (Figure 11.4). In 2012, at least 26 countries had established the national (or subnational) strategy and since then, nine²⁶ countries prepared their national strategy in response to the adoption of the Global Plan of Action (Figure 11.5). Of the 41 countries with national (or subnational) strategies for FGR conservation and use, six were unable to report the establishment year.

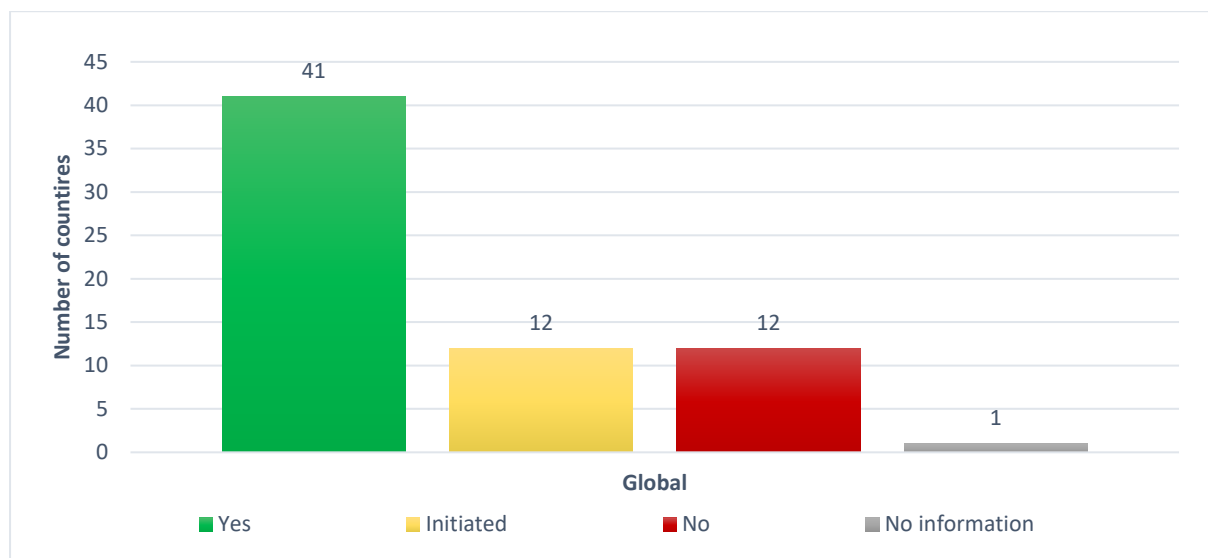


Figure 11.4 Number of countries with a national strategy (or subnational strategies) for FGR conservation and use.

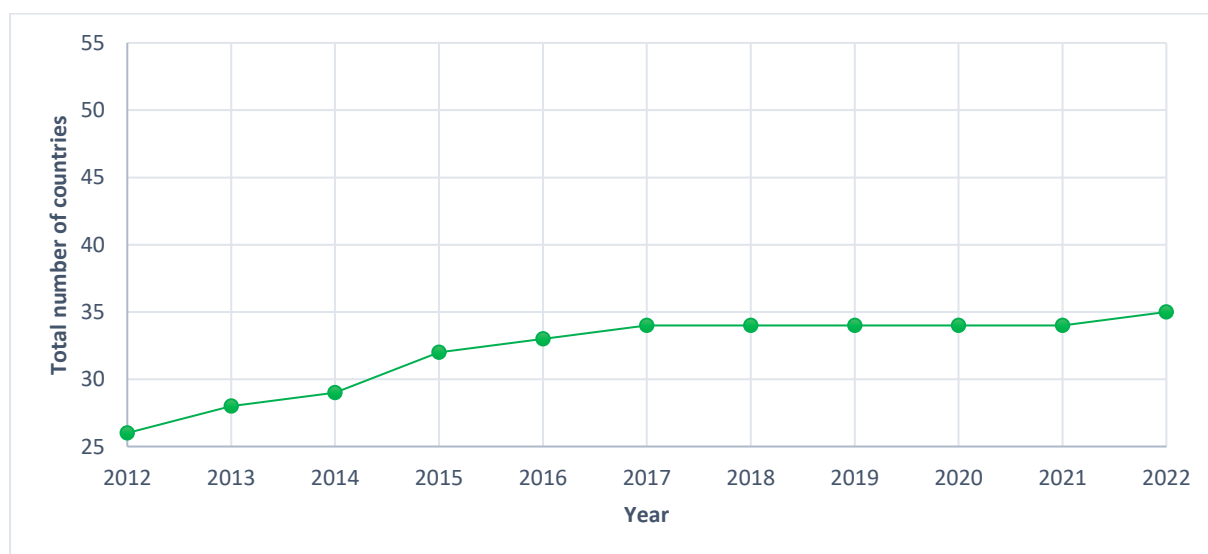


Figure 11.5 Development of national (or subnational) strategies for FGR conservation and use.

Most of the national strategies cover multiple areas of work; FGR conservation receives most attention (reported by 39 countries), followed by FGR use (32) and FGR development (26) (Figure 11.6).

²⁶ China, Ecuador, India, Ireland, Japan, Kenya, Lao People's Democratic Republic, Serbia and Sweden

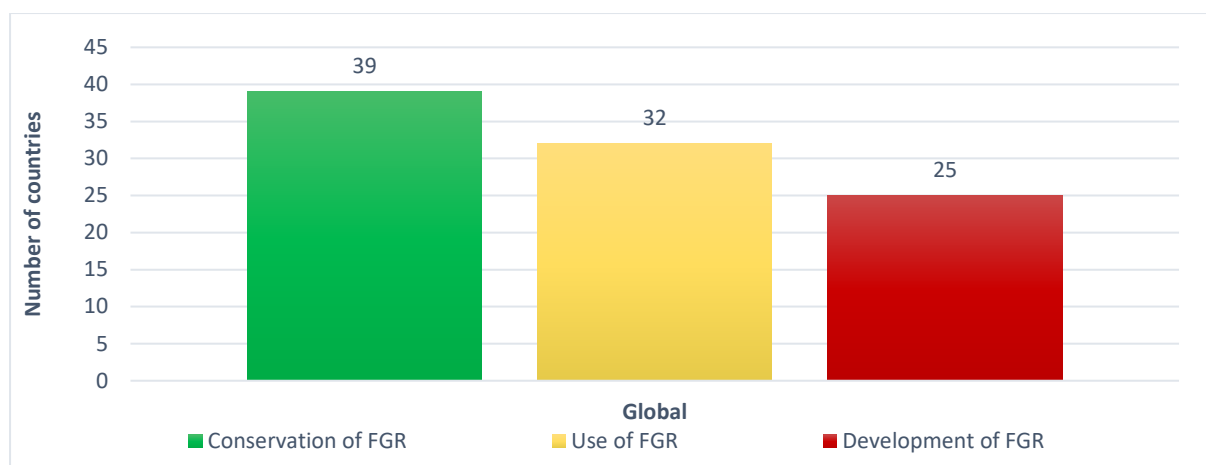


Figure 11.6 Areas of work covered by national (or subnational) strategies for FGR conservation and use.

The first national strategy on FGR dates to 1948 (Italy), and a recent example is Ireland’s Sustainable Development and Conservation of Forest Genetic Resources 2020-2030 Strategy.²⁷ The Irish strategy includes actions on the development and deployment of FRM with climate change considerations, FGR sector development, and genetic conservation of native tree species, for example.

In other countries, the national strategies have been prepared to address specific aspects of FGR, for instance *in situ* and *ex situ* conservation of native tree species at the national or regional level. Some countries also reported that, although they have a national strategy on FGR in place, its implementation has not yet fully started due to a lack of resources (e.g. Serbia). Countries that have not yet prepared a national strategy on FGR reported taking some strategic action in a more “integrated” manner.

11.3.2. Integration of FGR conservation and use into relevant national policies

The first global assessment revealed that national policies and programmes often insufficiently reflect FGR (FAO, 2014a), and the Global Plan of Action called for reviewing and updating relevant national policies, programmes, legal frameworks and regulations to integrate FGR (FAO, 2014b). FAO has prepared voluntary guidelines promoting the integration of FGR into national forest policies and national forest programmes (NFPs) (FAO, 2023), and prepared technical guidance to support the integration of FGR into national strategies related to biodiversity (FAO, 2021; FAO, 2020a) and climate change adaptation and mitigation (FAO, 2022; FAO, 2017a; FAO, 2017b; FAO, 2015).

For the preparation of this second assessment, 47 countries reported having integrated FGR conservation and use into national forest programmes and/or national forest policies, and nine countries reported having initiated a process for this (Figure 11.7). A total of 52 countries reported having integrated FGR conservation and use into national biodiversity action plans (NBSAP) and/or related policies, and five countries reported having initiated a process for this (Figure 11.8). Concerning national adaptation strategies for climate change, 33 countries reported having integrated FGR conservation and use into them, and 16 countries reported having initiated a process for this (Figure 11.9).

²⁷ <http://www.coford.ie/media/coford/content/publications/2020/35769COFORDbodyreportweb211220.pdf>

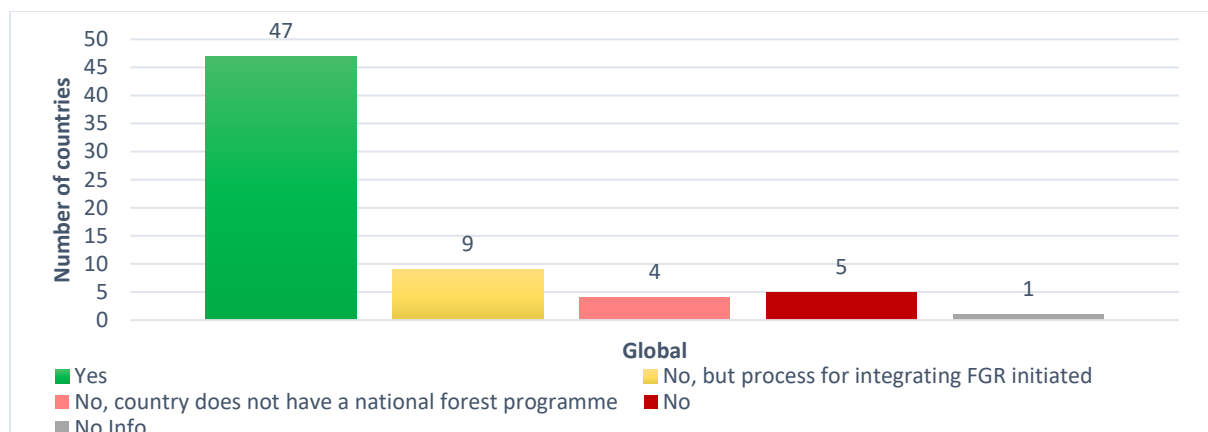


Figure 11.7 Number of countries with FGR conservation and use integrated into national forest programmes and/or national forest policies.

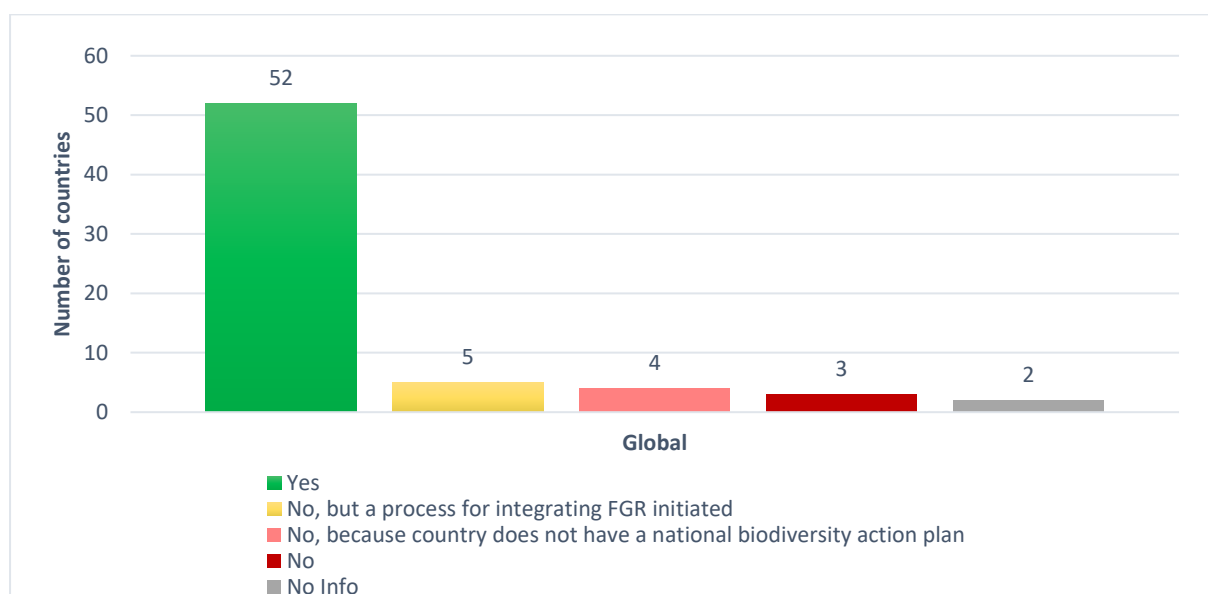


Figure 11.8 Number of countries with FGR conservation and use integrated into national biodiversity action plans and related policies.

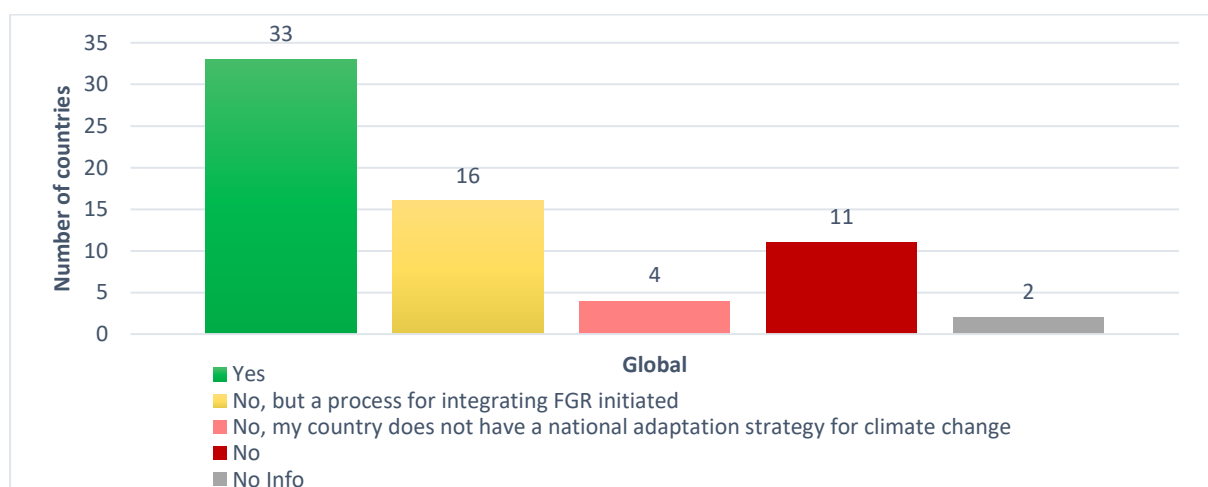


Figure 11.9 Number of countries with FGR conservation and use integrated into national adaptation strategies for climate change.

The level of integration varies considerably within countries. An example of FGR integration to a “high” level of specificity is the formulation of priorities and actions to operationalize goals related to FGR conservation, use and/or development. A “low” level of specificity of FGR integration is typically expressed as a general acknowledgement of the importance of FGR in relation to broader goals on forests, biodiversity and climate change. For example, Bulgaria mentioned concrete actions on FGR under its Forestry Strategy and Action Plan. Malta reported that FGR is integrated into NBSAP and that a NBSAP sub-strategy “Trees & Woodlands National Strategy and Action Plan” (TWNSAP) was developed. Estonia reported that FGR activities have been formulated under both the National Forest Development Plan and the National Climate Change Adaptation Plan. Australia reported that its Nature Conservation Strategy 2019-2030 integrates FGR under Goal 2 on “care for nature in all its diversity”. Germany reported that FGR and other agrobiodiversity sectors were integrated into the broader national strategy on biodiversity (NBSAP) with the support of its national working group on FGR “Leander BLAG-FGR”.

In addition to the level of FGR integration in relevant policies, some additional observations can be made. In the case of forest policies, it seems that FGR is often narrowly interpreted as part of biodiversity conservation. Many countries reported the integration of FGR conservation into protected area designation and management, while the role of production forests was not considered. A recent study by Harrison *et al.* (2022) highlights this gap and proposes including FGR in the management of production forests in multiple ways. Regarding FGR integration into biodiversity-related policies, an assessment of 114 NBSAPs revealed that although genetic diversity is deemed important, it is often overlooked and narrowly interpreted in NBSAP implementation, monitoring and reporting efforts at the national level (Hoban *et al.*, 2021). Similarly, another paper by Hoban *et al.* (2023) on genetic diversity in the CBD’s Kunming-Montreal Biodiversity Framework stressed the importance of clear and quantifiable global goals and targets on genetic diversity, and the consistent, effective and measurable implementation of genetic conservation at national level through improved NBSAPs and related strategies.

The findings of this second assessment indicate that progress has been made in integrating FGR into relevant national policies, programmes and strategies. Of the reporting countries, 66 percent have developed a national strategy on FGR that, in most cases, covers multiple areas of work (conservation, use and development). FGR conservation is more frequently integrated in relevant national strategies as compared to FGR use and development. The two main approaches to the development of a national strategy on FGR are the “stand-alone” and the “integrated” approaches. FGR considerations are better integrated into national policies on forests and biodiversity than national adaptation strategies to climate change. The way FGR considerations have been integrated into relevant national policies varies in terms of level of specificity, ranging from a concrete set of actions on FGR to more general acknowledgement of FGR importance.

11.4. Capacity building and education on FGR conservation, use and development

The first global assessment stressed that the availability of trained and skilled professionals as a determining factor for FGR conservation, use and development (FAO, 2014a), and the Global Plan of Action called for actions on capacity building and education related to FRG, as well as increased resources, such as field and laboratory equipment (FAO, 2014b).

As part of the FAO’s Global Forest Education (GFE) Project²⁸, regional assessments were prepared on the state of forest education, including to what extent FGR are covered in respective education curricula at the technical and vocational education and training (TVET), Bachelor’s and Associate’s ,

²⁸ <https://www.fao.org/forestry/forest-education/99204/en/>

and Master's and Doctoral levels.²⁹ Respondents comprised forest professionals³⁰, teachers and students. This section presents the findings of these regional assessments on the coverage of FGR in forest education in Africa (Kung'u, Muchiri and Kuria, 2021), Asia-Pacific (Shanahan *et al.*, 2021), Europe (Rekola, Nevgi and Sandström, 2021), Latin America and the Caribbean (Rodriguez-Piñeros, 2021), Near East and North Africa (FAO and AOAD, 2021) and North America (Sharik and Saracina, 2021). The findings are summarized below for TVET, Bachelor's and Associate's, and Master's and Doctoral levels.

TVET is a type of formal education generally delivered at secondary and tertiary level and focused on profession-based learning and specialized skill transfer to respond to current and future needs.³¹ Regarding the extent of FGR coverage in TVET education, most respondents in all six regions considered that FGR is inadequately covered in their TVET curriculum. When analysed by respondent group, most professionals and teachers across the regions rated FGR coverage as inadequate, while most students across regions (except Asia-Pacific) rated FGR coverage as sufficient.

Regarding FGR coverage in curricula at Bachelor's and Associate's levels, most respondents considered that FGR is sufficiently covered in their curricula, and this emerged from professionals, teachers and students equally. Regional exceptions are Latin America and the Caribbean and Near East and North Africa, where most respondents indicated that FGR was inadequately covered in their Bachelor's and Associate's curricula. It must be noted that in regions where most respondents found FGR coverage sufficient, such as North America, FGR is nonetheless considered a topic that needs more attention (Sharik and Saracina, 2021).

Concerning FGR coverage in curricula at Master's and Doctoral levels, findings are more varied across and within regions. In Africa and Near East, the majority of respondents reported that FGR is covered inadequately, while in the Asia-Pacific, Europe and North America regions, FGR coverage is generally considered sufficient. In Latin America and the Caribbean, there are variations in the findings among professionals, teachers and students; a relatively high percentage of professionals (more than 70 percent) rated FGR coverage as inadequate compared to lower percentages among teachers (50 percent) and students (45 percent). This may be due to the fact that professionals are better aware of the needs and requirements in the forest sector and the job market as compared to teachers and students.

Across TVET, Bachelor's and Master's levels, when FGR coverage was rated "sufficient", it was based on a slim margin (only 50 to 60 percent). In fact, among the 41 topics assessed, FGR rank high, and in some cases highest, across all six regions in terms of inadequate coverage. Therefore, all regional reports recommend increasing FGR coverage in forest education across all levels. Examples of recommendations include the delivery of training on seedlings identification, evaluation and assessment (Sharik and Saracina, 2021), and the creation of opportunities for professionals and students to acquire technology-based skills and familiarize themselves with new technologies such as tree genetics (Shanahan *et al.*, 2021).

The country reports submitted for the preparation of this global assessment also suggest that FGR education is seldom well-covered or a stand-alone discipline at the TVET, secondary and tertiary education levels. In most countries, FGR education is often delivered in an "integrated" manner, i.e. FGR-related topics are covered in a course (or course module) as part of broader, interdisciplinary curricula related to natural resource management, silviculture, forest management, forest engineering,

²⁹ "to what extent are the following topics covered in your [TVET/Bachelor's/Master's] education programme?" (three answers available: inadequately, sufficiently or excessively covered)

³⁰ Working with government agencies, NGOs, forest owners' associations, business organisations and labour unions

³¹ "TVETipedia Glossary". UNESCO-UNEVOC. UNESCO. Retrieved 30 December 2022. <https://unevoc.unesco.org/home/TVETipedia+Glossary/lang=en/filt=all/id=474>

biology or plant breeding. Such course or module may include a field or laboratory component. Several countries, such as Canada, Serbia and Switzerland, reported stand-alone university courses on FGR.

Most countries mentioned a gap between education curricula and the field-level needs of FGR users and the forest sector. Sweden is one of the few countries that reported a specialized, stand-alone education programme on FGR, called the Industrial Graduate Student Research School of Forest Genetics, Biotechnology and Breeding.³² It is a 5-year postgraduate academia-industry programme, established in 2013, and covering molecular genetics of prioritized traits, genomics, somatic embryogenesis, statistics, quantitative genetics and breeding theory.

Overall, countries noted a decline in enrolments in forest-related programmes. Reasons for declining popularity of forest education include reduced attractiveness and financial support and a perceived mismatch between forestry curricula and the current labour market. These reasons correspond with the findings from the GFE project and its regional assessments (Rekola and Sharik, 2022). A notable exception is Brazil, which reported an increase in the number of courses and the degrees on forest-related topics between 1995 and 2021. Moreover, the country's courses and degrees have a regional and international reach in terms of student enrolments.

The findings of the GFE regional assessment on FGR coverage in forest education show that the topic of FGR is inadequately taught across all six regions and highlight the need to improve the coverage of FGR in forest curricula at all levels. The country reports support these findings and call for improved FGR education, especially at TVET level, to train professionals and students to respond to the current and future needs of the forest sector and support FGR stakeholders with field-level activities. Interesting developments were reported in Brazil with increased forest-related courses, degrees and enrollments during the past 25 years, and in Sweden with the establishment of a post-graduate programme on FGR.

11.5. Conclusions

The first global assessment on FGR and the Global Plan of Action called for strengthening of the institutional framework for the conservation, use and development of FGR. The findings of this report show that progress has been made in this regard, and in relation to national coordination mechanisms, national strategies for FGR, integration of FGR into relevant national policies, and capacity building on FGR.

The findings also indicate a continued need for countries to continue strengthening their institutional frameworks, i.e. their national coordination mechanisms, national strategies on FGR, the integration of FGR into relevant national policies, and FGR education and capacity building. In identifying possible actions for the strengthening of the institutional framework to promote FGR conservation, use and development, countries are encouraged to consider all areas of FGR work, to engage all relevant stakeholders, and to take specific actions on FGR. The broad range of national (or subnational) institutional frameworks reported highlight the institutional complexity and cross-sectoral nature of FGR governance. It is also necessary to take into consideration all relevant stakeholders and their needs and priorities in developing adequate national institutional frameworks for the conservation, use and development of FGR.

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[CHAPTER 12. INTERNATIONAL AND REGIONAL COOPERATION ON FOREST GENETIC RESOURCES]

PART 6: CHALLENGES AND OPPORTUNITIES

CHAPTER 13. RECOMMENDED ACTIONS FOR THE FUTURE

13.1. Introduction

The first-ever global assessment on forest genetic resources was prepared 10 years ago (FAO, 2014a) and its findings paved the way for the adoption of the Global Plan of Action for these resources by the FAO Conference in 2013 (FAO, 2014b). This second global assessment was prepared at the request of the Commission on Genetic Resources for Food and Agriculture to analyse how the state of the world's forest genetic resources might have changed since then, and to monitor the progress made in the implementation of the Global Plan of Action.

A decade is a relative short period of time, especially when compared to the long lifespan of forest trees and other wood species. The overall state of the world's forests has changed little during this period, as demonstrated by the fact that forests still cover 31 percent of the world's total land area (FAO, 2020). Unfortunately, deforestation continued with the annual rate of net forest loss of 4.17 million hectares between 2010 and 2020 (FAO, 2020). As a new development, the results of a global remote sensing survey now provide a more detailed picture on deforestation in different forest biomes (FAO, 2022). This survey also found that almost 90 percent of deforestation between 2000 and 2018 was driven by the conversion of forests to cropland and livestock grazing. Another new development was the global assessment of tree species, which documented over 58 000 tree species in the world (BGCI, 2023) as compared to the earlier estimates which ranged between 50 000 and 100 000 species (see FAO, 2014a).

Concerning forest genetic resources themselves, this second global assessment found that many actions have been taken at national, regional and international level to implement the Global Plan of Action. Its findings provide a more refined picture on the state of conservation, use and development of forest genetic resources in the world as compared to the first assessment, and show that progress has been made under all four priority areas of the Global Plan of Action, albeit to varying degrees. However, the present findings do not allow detailed quantification of how much the state of the world's forest genetic resources might have improved during the past decade. The main reason is that the reporting requirements for this second assessment were somewhat different from those used for the preparation of the first one.

The following sections present, based on the four priority areas of the Global Plan of Action, some suggestions for recommended actions for the next decade.

13.2. Availability of, and access to, information on forest genetic resources

The long-term goal of Priority Area 1 was designed to “improve the availability and accessibility of knowledge and information on species and their genetic diversity, forest ecosystems and related traditional knowledge, to facilitate and enable decision-making on sustainable use and management of forest genetic resources” (FAO, 2014b). It further aims to “enhance their contribution to solving serious global problems such as food shortage, land and water degradation, the effects of climate change, and increased demand for various forest products and services”.

While several countries have made progress towards this goal by gathering better information on their forest genetic resources, and in establishing national information systems, the preparation of this report showed that the information on forest genetic resources is still scattered in many countries, both developing and developed ones. Most of the reporting countries (68 percent) have a national inventory on these resources or a similar arrangement in place, and 59 percent of the countries have created a national information system. However, it seems that these mechanisms do not always connect to, or gather data from, all stakeholders that are involved in the management of FGR at national level. These gaps mean that many countries do not have a clear picture of the status of their forest genetic resources, and of the efforts made to conserve and manage them. If not improved, this situation will continue hampering any future global assessment on forest genetic resources. Countries were able to report their responses to the Global Plan of Action in terms of various mechanisms and programmes

but struggled to provide species-specific data on their efforts to conserve, use and develop the genetic resources of trees and other woody species.

The preparatory process of the second global assessment, and especially the regional meetings organized for the National Focal Points and other national experts, allowed to increase understanding on the technical terms, concepts and approaches related to the conservation, use and development of forest genetic resources. Furthermore, the criteria, indicators and verifiers adopted by the Commission for monitoring the implementation of the Global Plan of Action proved a useful first step for harmonizing the data collection for the global assessment. However, some indicators and verifiers are still interpreted in different ways by the National Focal Points, indicating the need to continue efforts towards a common understanding of the technical aspects and the reporting requirements for the future global assessments. The preparatory process also revealed that the term *forest genetic resources* itself and species related to this term are understood differently by countries.

In parallel with the preparation of the second assessment, FAO made progress in developing the new global information system in collaboration with the National Focal Points. Once launched, the information system will make available the data and information gathered for this report, and hopefully it will be used in the future not only for the international reporting on forest genetic resources but also for supporting and strengthening countries' own efforts in managing these resources. The new information system will also offer an opportunity for countries to continue frequently updating the data and information without waiting for the next reporting process. Moreover, it will complement many regional and global information systems developed and maintained by regional networks and international organizations.

13.3. *In situ* and *ex situ* conservation of forest genetic resources

The long-term goal of Priority Area 2 aims to “maintain genetic diversity and the evolutionary processes of forest species by better implementing and harmonizing measures to conserve forest genetic resources, both *in situ* and *ex situ*, including through regional cooperation and networking” (FAO, 2014b).

The findings of the present report show that progress has also been made towards this goal. However, they indicate that the efforts have focused more on *in situ* conservation and that little progress has been made in *ex situ* conservation. Currently, 88 percent of the reporting countries have a national *in situ* conservation system (or systems) in place, and at five countries established such a system during the past decade. In comparison, 76 percent of the countries currently have a national *ex situ* conservation system in place, but no country established such system between 2012 and 2022.

The number of species included in the conservation programmes also suggests that more efforts focused on conserving forest genetic resources *in situ* than *ex situ*. The *in situ* conservation programmes reported for this global assessment include 1 283 species (66 countries), while the same figure was nearly 1 000 (86 countries) a decade ago (FAO, 2014a). The reported *ex situ* conservation programmes now include 978 species while the same figure was around 1 800 species ten years (FAO, 2014a).

The present findings confirm that *in situ* conservation remains the preferred approach for conserving forest genetic resources because of the key features of forest trees and other woody species (see FAO, 2014b for a summary). The findings also show that most countries rely on protected areas as the key component of their *in situ* systems. However, recent studies in different regions show that valuable forest genetic resources are found outside of protected areas, highlighting the need to continue complementing protected areas with other conservation units and managed forests. This would also enhance the use of forest genetic resources while they are being conserved outside protected areas. While *ex situ* conservation is often considered as a complementary measure to *in situ* conservation of forest genetic resources, it remains equally important element as it provides a win-win situation for both conservation and use.

The conservation efforts can now benefit from advanced molecular and genomic tools. In addition, sophisticated spatial tools are also available for setting priorities in the practical conservation work, and genetic and genomic data, including range-wide characterizations of genetic diversity, are available for more species as compared to 10 years ago. Regional networks have also played an active role in identifying priority species and developing regional *in situ* conservation strategies. Despite these positive developments, the lack, or limited availability, of species-specific data in many countries related to their conservation programmes raises some concerns on the coverage and effectiveness of the conservation efforts. Therefore, it is necessary to continue efforts under this priority area at national and regional level.

[13.4. Sustainable use, development and management of forest genetic resources]

13.5. Policies, institutions and capacity-building

The long-term goal of Priority Area 4 aims to “establish and review relevant policies and legal frameworks in order to integrate major issues related to sustainable management of forest genetic resources, and to strengthen institutional and human capacity” (FAO, 2014b).

During the past decade, many countries took action related to national strategy for the conservation and use of forest genetic resources. The integration of forest genetic resources into relevant national policies has also advanced, in particular into national forest policies and national biodiversity action plans. However, only 50 percent of the countries reported having integrated forest genetic resources into national adaptation strategies for climate change. The level of integration varies considerably within countries, from being mentioned or acknowledged to specific actions on forest genetic resources included in relevant national strategies. As part of future integration efforts, it would be important to promote the latter approach.

A national coordination mechanism on forest genetic resources is now operational in 58 percent of the countries, and the majority of these coordination mechanisms engage multiple stakeholder groups, as recommended by the Global Plan of Action. However, the main stakeholders are typically governmental organizations, research organizations and relevant ministries, suggesting that the coordination mechanism would benefit from a wider participation of stakeholders in the future.

The findings of the present report indicate that human and institutional capacities related to forest genetic resources remain weak. Overall, forest education is in decline, and it covers inadequately these resources across all regions. The country reports called for improved education on forest genetic resources, especially at the level of technical and vocational education and training. Therefore, special emphasis should be given to the development of human and institutional capacities in this area during the next decade.

Regional and international cooperation is active worldwide, and regional networks and international organizations play an important role in providing technical, and sometimes financial, support to the management of forest genetic resources at national level. In some regions, however, the regional collaboration could be strengthened, and the many tools and knowledge products developed by regional networks and international organizations better disseminated to relevant stakeholders on the ground.

Public and international awareness of the roles and values of forest genetic resources remain low despite various efforts. It is also evident that the available human and financial resources available for the actions on forest genetic resources are inadequate in many countries and in particular developing countries. It is thus crucial to continue efforts to raise awareness of the importance of forest genetic resources and to mobilize the necessary resources to support the implementation of the Global Plan of Action.

[13.6. Conclusions]**[13.7. References]**

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[ANNEXES]