



Global to local genetic diversity indicators of evolutionary potential in tree species within and outside forests



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ABSTRACT

There is a general trend of biodiversity loss at global, regional, national and local levels. To monitor this trend, international policy processes have created a wealth of indicators over the last two decades. However, genetic diversity indicators are regrettably absent from comprehensive bio-monitoring schemes. Here, we provide a review and an assessment of the different attempts made to provide such indicators for tree genetic diversity from the global level down to the level of the management unit. So far, no generally accepted indicators have been provided as international standards, nor tested for their possible use in practice. We suggest that indicators for monitoring genetic diversity and dynamics should be based on ecological and demographic surrogates of adaptive diversity as well as genetic markers capable of identifying genetic erosion and gene flow. A comparison of past and present genecological distributions (patterns of genetic variation of key adaptive traits in the ecological space) of selected species is a realistic way of assessing the trend of intra-specific variation, and thus provides a *state indicator* of tree genetic diversity also able to reflect possible *pressures* threatening genetic diversity. Revealing benefits of genetic diversity related to ecosystem services is complex, but current trends in plantation performance offer the possibility of an indicator of *benefit*. *Response* indicators are generally much easier to define, because recognition and even quantification of, e.g., research, education, breeding, conservation, and regulation actions and programs are relatively straightforward. Only *state* indicators can reveal genetic patterns and processes, which are fundamental for maintaining genetic diversity. Indirect indicators of *pressure*, *benefit*, or *response* should therefore not be used independently of *state* indicators. A coherent set of indicators covering diversity–productivity–knowledge–management based on the genecological approach is proposed for application on appropriate groups of tree species in the wild and in cultivation worldwide. These indicators realistically reflect the state, trends and potentials of the world's tree genetic resources to support sustainable growth. The state of the genetic *diversity* will be based on trends in population distributions and diversity patterns for selected species. The *productivity* of the genetic resource of trees in current use will reflect the possible potential of mobilizing the resource further. Trends in *knowledge* will underpin the potential capacity for development of the resource and current *management* of the genetic resource itself will reveal how well we are actually doing and where improvements are required.

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1. Introduction

The development of biodiversity indicators to track the rate of loss of biodiversity on a global scale has been underway for over two decades, first with the adoption of the Convention on Biological Diversity (CBD¹) in 1992 (SCBD, 2001), followed in 2002 (SCBD, 2006) by the agreement on targets to reduce the loss of biological diversity by 2010 (the 2010 Biodiversity Target), and most recently in 2010, by the adoption of the Aichi Targets and a revised and updated Strategic Plan for Biodiversity 2011–2020 (UNEP/CBD/COP, 2010).

The rationale behind this work is a general recognition of the richness of biological diversity on Earth, the threats that human activities pose to this richness, and the negative consequences that further loss of diversity may have to mankind and to the Earth biomes as a whole. The objectives of CBD refer to intrinsic and utilitarian values of biodiversity, including their importance for evolution and maintaining life-sustaining systems (Glowka et al., 1994). Its overarching goal of sustainable development is to ensure and enhance the livelihoods of millions of people under the challenge of balancing the human appropriation of nature with the effects of global climate change and a growing world population.

According to CBD, biological diversity embraces the diversity of all life on Earth and is commonly distinguished at three levels: ecosystems, species, and genes. The values of biodiversity are generally associated with these levels. Environmental and life-support values are typically provided at ecosystem level, material goods at species level and the improvement of production depends on the availability of genetic variation (FAO, 1989). The idea of identifying biodiversity indicators is therefore not merely tracking the loss of biodiversity, although this is used as the relevant overall measure, but also to enable priority setting for conservation, development and sustainable use of biodiversity.

Criteria and indicators are used in different fields of human enterprise to define priorities and measure the extent to which these priorities are met (e.g. Prabhu et al., 1999). They have become an instrument of choice for national and international organizations to guide their members (and attract membership) towards common, quantifiable goals. The focal area of sustainable forest management, for example, relies strongly on criteria and indicators to monitor progress (Wijewardana, 2006). A criterion usually reflects an objective (also termed goal or target), often rather complex and challenging to assess; in our case, the degree to which the genetic diversity of the world's forests and trees is conserved. Practical and informative indicators which can be measured periodically to reveal the direction of change of a variable (the genetic diversity of world forests in our example) are therefore required. Indicators are, by definition, used to track progress and should always be defined in relation to a given target (Feld et al., 2009). An indicator must be measurable and the metric used to measure an indicator is commonly referred to as a verifier.

Although important progress has been made overall, there is “still a considerable gap in the widespread use of indicators for many of the multiple components of biodiversity and ecosystem services, and a need to develop common monitoring schemes within and across habitats” (Feld et al., 2009). In a scientific assessment, Butchart et al. (2010) compiled 31 indicators to report on the progress of the 2010 Biodiversity Target. They concluded that, despite some local successes and increasing responses (e.g., in terms of protected area coverage), the rate of biodiversity loss does not appear to be slowing (Butchart et al., 2010).

Here, we are concerned with genetic diversity, which is not explicitly defined in CBD, and in particular, we focus on trees.

Genetic diversity is defined here as the total amount of genetic differences within species. It is also referred to as intra-specific variation. Intra-specific variation can be subdivided into inter- and intra-population variation (also among and within population genetic diversity), and further into the diversity within an individual expressed by differences between alleles across chromosomes. Genetic diversity is a major element of biodiversity (CBD Article 2), it is the basis for adaptation and it has been recognized by the Millennium Ecosystem Assessment (MEA, 2005) for its support to ecosystem functioning. Nevertheless, it is still rarely considered and only a few global or regional indicators make reference to it (Nivet et al., 2012).

Genetic diversity is probably the element of biodiversity for which the development of relevant indicators is least advanced. In their 2009 review of 617 peer-reviewed journal articles between 1997 and 2007, Feld et al. (2009) were able to list 531 indicators for biodiversity and ecosystem services encompassing a wide range of ecosystems (forests, grasslands scrublands, wetlands, rivers, lakes, soils and agro-ecosystems) and spatial scales (from patch to global scale). They found that “despite its multiple dimensions, biodiversity is usually equated with species richness only”, mostly at regional and finer spatial scales. Regional to global scale indicators were less frequent than local indicators and mostly consisted of physical and area fragmentation measures. Despite their role and potential value across scales and habitats, “functional, structural and genetic components of biodiversity [were] poorly addressed”. Genetic diversity was included in less than 5% of the 531 biodiversity indicators analyzed.

This lack of genetic diversity indicators has repeatedly been pointed out by the scientific community (e.g. Laikre, 2010; Laikre et al., 2010). It has been recognized by the Secretariat of the Convention on Biological Diversity (SCBD, 2010, cf. also Walpole et al., 2009) and the Strategic Plan for Biodiversity 2011–2020 allows for improved coverage of genetic diversity.

Genetic diversity is – or has been – perceived as complex and costly to measure and the task of identifying relevant indicators therefore considered close to impossible. At present, the genetic diversity of terrestrial domesticated animals reported by FAO and the International Livestock Research Institute (ILRI) is the only indicator reported under Aichi Target 13 on genetic diversity (Chenery et al., 2013, Biodiversity Indicators Partnership, BIP, 2013). A few additional indicators of relevance to genetic diversity are reported within the BIP (cf. Chenery et al., 2013; BIP, 2013). Although genetic diversity continues to be poorly covered, there are promising initiatives of application, primarily related to wildlife and the marine environment (Stetz et al., 2011; European Commission, 2011; CONGRESS, 2013).

Genetic diversity can be assessed by different techniques. Morphological and adaptive traits can be studied in field trials, and biochemical, molecular and DNA variants in the laboratory. Such studies contribute direct measures of intra-specific variation. In combination with knowledge of eco-geographic variation and history, genetic studies can be used to establish possible evolutionary patterns as well as recommendation domains for deployment of reproductive material in production systems.

Molecular markers are either influenced by selection or not (in which case they are termed neutral), whereas quantitative variation measured in field trials is usually adaptive. Both types of technique are important to gain knowledge of genetic patterns and processes. The use of molecular tools for genetic monitoring has moved from an era of scepticism (McKinnel, 2002), where studies were limited to revealing patterns of neutral genetic diversity, to a point of great promise of surmising also adaptive genetic variation (Funk et al., 2012; Hansen et al., 2012; Schwartz et al., 2007).

While field trials continue to be expensive and time consuming, the costs of genetic marker studies are decreasing. With increasing

¹ Abbreviations and acronyms are listed in Appendix A.

ability to handle large amounts of data and combine available information from genetic studies with other geographically based information, it now seems possible to suggest indicators of genetic diversity that are both relevant and not prohibitively costly.

The purpose of this paper is to provide a framework and a typology for the application of such indicators of tree genetic diversity commensurate with the current international scheme provided by the Strategic Plan for Biodiversity 2011–2020 and the BIP.

To do so, we first describe the Strategic Plan and the work of BIP to identify indicators within the established framework that are relevant for tree genetic diversity (Section 2). Next, a review of past attempts to define and report on possible tree genetic diversity indicators is provided, in order to reveal why they have not been widely applied (Section 3). We then move on to suggest what we consider meaningful and realistic indicators of genetic diversity of trees that can be embedded within the Strategic Plan and BIP, and constitute a framework and typology for management of trees within, as well as outside, forests (Section 4). Finally, conclusions (Section 5) are provided.

2. The framework of the Strategic Plan for Biodiversity 2011–2020

According to Sparks et al. (2011) and UNEP/CBD/AHTEG (2011a,b), indicators should ideally provide answers to, or shed light on, four basic questions (Table 1). In the case of tree genetic diversity, indicators should monitor the adaptive potential of tree species to help identify and prioritize actions, related to its use and conservation.

The UN Strategic Plan for Biodiversity 2011–2020 is made of five strategic goals and 20 specific targets to be achieved by 2020, referred to as the Aichi Targets (UNEP/CBD/COP, 2010, 2011). To monitor progress, an elaborate indicator framework for assessing the Aichi Targets has been developed by the Ad Hoc Technical Expert Group (AHTEG) on indicators for the Strategic Plan (UNEP/CBD/AHTEG, 2011a,b). This indicator framework consists of 12 proposed headline indicators and 97 proposed operational indicators (see Table 2 for examples). A single indicator, used in isolation, is generally considered insufficient to assess overall progress towards a target, thus the necessity to link multiple indicators (Chenery et al., 2013).

The global initiative BIP has been established to promote and coordinate development and delivery of biodiversity indicators in support of the CBD and other sectors. BIP brings together over 40 organizations working internationally on indicator development to provide the most comprehensive information on biodiversity trends (BIP, 2013).

Currently 29 operational indicators are reported under the 12 headline indicators, covering various aspects of 17 of the 20 Aichi Targets (BIP, 2013; Chenery et al., 2013). These 29 indicators typically relate (but are not identical) to one of the 97 AHTEG indicators in a further operational form. Although termed operational, most cases of the 97 AHTEG indicators will need to be transformed into specific verifiable “sub-topic” indicators that can actually be measured (cf. Table 2). It is important to note that the AHTEG framework is flexible enough to allow the transformation and

addition of indicators as needed. Types of indicators and indicators relevant for genetic diversity are described further in Appendix B.

The indicator sequence used by the UNEP/CBD/AHTEG (2011a,b) system is S–P–B–R, as it is considered to be the logical sequence of the four basic questions listed in Table 1. This is in contrast to the R–S–P–B sequence recommended by Sparks et al. (2011), who emphasize that response (rather than pressure) is the indicator that will be used to guide policy and practice. The sequence can be discussed and Sparks et al. (2011) therefore present the framework as a “feedback loop” subject to iterative modifications.

From the 97 operational indicators proposed by UNEP/CBD/AHTEG (2011a,b), we have selected those that we consider to have potential relevance for monitoring tree genetic diversity. They are all listed in Table 2, using the S–P–B–R sequence of UNEP/CBD/AHTEG (2011a,b).

In constructing Table 2, we followed the suggestions for headline indicators and operational indicators considered relevant (“most relevant” or “other relevant”) by UNEP/CBD/AHTEG (2011a,b) under the two Aichi Targets directly addressing genetic diversity (Targets 13 and 16), providing 14 operational indicators. These comprise only state and response indicators.

We have added those operational indicators that address tree species distribution, population trends and extinction risks, thus targeting intra-specific variation (cf. e.g., Rogers and Ledig, 1996; Bariteau, 2003), but not mentioned as such by UNEP/CBD/AHTEG (2011a,b). This provides an additional set of nine operational indicators, of which two are classified as state indicators, five as pressure indicators, and one each as a benefit and response indicator. In addition we have included three operational indicators that reflect benefit, value and condition of ecosystem services for adequate coverage of the benefits of genetic diversity. We have added one operational response indicator covering capacity building, knowledge transfer and uptake into policy, areas which are of obvious importance for the conservation, management and use of genetic diversity. Finally, we have included one operational response indicator related to awareness and public engagement without specifying a name of the operational indicator.

Thus, all 12 proposed headline indicators and 28 of the operational indicators proposed by UNEP/CBD/AHTEG (2011a,b) are considered relevant for genetic diversity in the context of the present study. The distribution of the indicators according to type and level of biodiversity targeted is summarized in Table 3.

Of the 28 operational indicators, 5 relate primarily to the ecosystem level, 11 to the species level, 4 to the intra-specific level, and 8 cut across levels. Among these 28 operational indicators, UNEP/CBD/AHTEG (2011a,b) considers 10 ready for use at the global level (class A), 11 are suggested for development at the global level (class B), 6 are proposed for consideration/development at sub-global level (class C, i.e. regional, national or local), and 1 is unclassified in terms of level, but relevant in general for all areas (cf. Table 2). The list of indicators relevant for genetic diversity of trees is thus considerable. However, translating headline and operational indicators of species’ distributions and their genetic diversity into specific verifiable sub-topic indicators remains a significant challenge.

Table 1

Indicators grouped into four types depending on the basic question they are intended to address and the actions that society can implement.

Basic question	Type of indicator	Intended significance of indicator
How is the status of biodiversity changing?	S – State	Analyzing the conditions and status – are we losing genetic diversity? Where, which and how?
Why is biodiversity being lost?	P – Pressure	Monitoring the extent and intensity of the causes of loss
What are the implications for society?	B – Benefit	Quantifying the benefits that humans derive from biodiversity and the costs of loss
What does society do about it?	R – Response	Measuring the implementation of policies or actions to prevent or reduce loss

Table 2
Relationships between the types of indicators (in the sequence of UNEP/CBD/AHTEG: S: state, P: pressure, B: benefit, and R: response), headline indicators and operational indicators of relevance for tree genetic diversity (Source: extracted and adapted from Appendix V in [UNEP/CBD/AHTEG, 2011a](#)). A: ready for use at the global level, B: recommended for development at the global level, C: proposed for consideration/development at the sub-global level. Aichi Target: “most relevant target” first; if Target 13 or 16 among “other relevant targets”, listed subsequently (see text). The level of diversity (ecosystem, species, intra-specific or general biodiversity) that is the focus of the indicator has been added.

Type of indicator	Headline indicator	Level and readiness for use	Operational indicator name	Aichi target number	Diversity focus
S	Trends in extent, condition and vulnerability of ecosystems, biomes and habitats	A	Extinction risk trends of habitat dependent species in each major habitat type	12	Species/ ecosystem
S	Trends in abundance, distribution and extinction risk of species	A	Trends in abundance of selected species (UNCCD indicator)	12,13	Species
		A	Trends in extinction risk of species (MDG indicator 7.7) (also used by CMS)	12,13	Species
		B	Trends in distribution of selected species (also used by UNCCD)	12	Species
S	Trends in genetic diversity of species	B	Trends in genetic diversity of cultivated plants, and farmed and domesticated animals and their wild relatives	13	Intra-specific
		C	Trends in genetic diversity of selected species	13	Intra-specific
P	Trends in pressures from unsustainable agriculture, forestry, fisheries and aquaculture	A	Trends in populations and extinction risk of utilized species, including species in trade (also used by CITES)	4	Species
		B	Trends in populations of forest and agriculture dependent species in production systems	7	Species
P	Trends in pressures from habitat conversion, pollution, invasive species, climate change, overexploitation and underlying drivers	A	Population trends of habitat dependent species in each major habitat type	5	Species
		A	Trends in the impact of invasive alien species on extinction risk trends	9	Species
		B	Trends in climate change impacts on extinction risk	10	Biodiversity
B	Trends in distribution, condition and sustainability of ecosystem services for equitable human well-being	A	Trends in benefits that humans derive from selected ecosystem services	14	Ecosystem
		A	Population trends and extinction risk trends of species that provide ecosystem services	14	Species
		B	Trends in economic and non-economic values of selected ecosystem services	14	Ecosystem
		C	Trends in the condition of selected ecosystem services	14	Ecosystem
R	Trends in awareness, attitudes and public engagement in support of biological diversity and ecosystem services	C	[3 indicators given in the source]	1	Biodiversity (general)
R	Trends in integration of biodiversity, ecosystem services and benefit sharing into planning, policy formulation and implementation and incentives	B	Trends in number of effective policy mechanisms implemented to reduce genetic erosion and safeguard genetic diversity related to plant and animal genetic resources	13	Intra-specific
		B	Trends in implementation of National Biodiversity Strategies and Action Plans, including development, comprehensiveness, adoption and implementation	17,13,16	Biodiversity
R	Trends in access and equity of benefit sharing (ABS) of genetic resources	B	ABS indicator to be specified through the ABS process	16	Intra-specific
R	Trends in accessibility of scientific/technical/traditional knowledge and its application	B	Trends in degree to which traditional knowledge and practices are respected through: full integration, participation and safeguards in national implementation of the Strategic Plan	18,13	Biodiversity
		B	Trends in coverage of comprehensive policy-relevant sub-global assessments including related capacity building and knowledge transfer, plus trends in uptake into policy	19	Biodiversity
		C	Number of maintained species inventories being used to implement the Convention	19,13	Species
R	Trends in coverage, condition, representativeness and effectiveness of protected areas and other area-based approaches	A	Trends in protected area condition and/or management effectiveness including more equitable management (decision X/31)	11,13	Biodiversity (protected areas)
		A	Trends in representative coverage of protected areas and other area-based approaches, including sites of particular importance for biodiversity, and of terrestrial, marine and inland water systems	11,13	Ecosystem
		B	Trends in the connectivity of protected and other area based approaches integrated into land- and sea-scapes (decision VII/30 and VIII/15)	11,13	Biodiversity (protected areas)
		C	Population trends of forest-dependent species in forests under restoration	15	Species
		C	Trends in the delivery of ecosystem services and equitable benefits from protected areas	11,13	Ecosystem
R	Trends in mobilization of financial resources	Not specified	Trends in financial flow of funding for implementation of the Strategic Plan [Indicators agreed in decision X/3 of CBD COP]	20,16	Biodiversity

Table 3

Number and type of indicators proposed by [UNEP/CBD/AHTEG \(2011a\)](#) considered of relevance for tree genetic diversity and the primary level of diversity targeted (ecosystem, species, genes (intra-specific) or biodiversity in general), cf. Table 2.

Type/target	Ecosystem	Species	Intra-specific	Biodiversity	Total
S – state	1	4	2	0	7
P – pressure	0	4	0	1	5
B – benefit	3	1	0	0	4
R – response	1	2	2	7	13
Total	5	11	4	8	28

3. What has been done and why have indicators of tree genetic diversity not been widely applied to date?

3.1. Sustainable forest management and indicators of tree genetic diversity

Hardly any of the CBD biodiversity indicators have yet found use in the forestry sector. Trends in the extent of forest and forest types are reported by FAO under Aichi Target 5 concerning loss of habitats, and the area of forest under certified forest management is reported by the [Forest Stewardship Council \(FSC\)](#) under Aichi Target 7 concerning areas under sustainable forest management ([Chenery et al., 2013](#); [BIP, 2013](#)). However, neither of these allows inference on the loss of genetic diversity within tree species.

In parallel with the work of CBD, a process for monitoring and promoting conservation of forest biodiversity through sustainable forest management has taken place within the framework of the UN Forest Forum (UNFF) ([Rosendal, 2001](#); [FAO, 2002](#)). Consequently, several international criteria and indicator processes have been initiated for forests and many of these have made an attempt to identify indicators of genetic diversity as part of a larger set of biodiversity indicators. A summary and an analysis of these indicators are given in [Appendix C](#).

Considerable efforts have been employed for defining and implementing indicators of sustainable forest management, but few relate directly to tree genetic diversity. The most significant are probably the sustainable management schemes developed by FSC and the Programme for the Endorsement of Forest Certification (PEFC), the two largest certification systems worldwide, which have been endorsed by numerous organizations (both for conservation and use). Several of the generic principles and criteria of both of these certification systems relate to genetic diversity. However, as both FSC and PEFC criteria and indicators of sustainable management are generic, there is considerable space for discussion on how they are applied locally ([Auld and Aitken, 2003](#)). Furthermore, indicators for sustaining genetic diversity are considered difficult to measure, costly and tend to not be implemented ([Parviainen and Lier, 2006](#); [Wijewardana, 2006](#); [Anon, 2011](#); [Aravanopoulos, 2011](#)). Among the countries participating in the Montreal Process there was “no scientific agreement on how the data should be collected” and “little or no understanding of how to measure an indicator” ([Parviainen and Lier, 2006](#)).

To date, the limited action taken to assess efforts to conserve genetic diversity of trees has been indirect and almost entirely related to response indicators. While tree genetic diversity can be correctly managed and protected in FSC- or PEFC-certified forests or in protected areas, there is no guarantee that it will be. Reporting on response indicators alone without measuring state indicators (as, for example, in the Pan European Process, [Forest Europe et al., 2011](#); [Nivet et al., 2012](#)) can result in misleading conclusions because well-intentioned policies and management practices do not necessarily result in an improved conservation status for tree genetic diversity. Overall, in particular, the identification of state indicators at the global level remains a major challenge.

3.2. Global surveys of forest genetic resources

A global programme for conservation and management of forest genetic resources was initiated by FAO early in the 1960s ([FAO, 1975](#)) and several regional networks on forest genetic resources were established at the initiative of FAO and Bioversity International (then as IBPGR, later IPGRI) in the late 1980s and early 1990s. During that period, several reviews of the state of forest genetic resources covering different geographical areas were prepared ([Palmberg-Lerche, 2007](#)), and a wealth of reports is available ([FAO Forest Genetic Resources Working Papers, 2013](#)). However, in general, the information about characterization of genetic diversity is more descriptive than quantitative. A survey in the early 1990s led to the establishment of REFORGEN ([FAO Forest Genetic Resources REFORGEN Database, 2013](#)), but it also contains little quantitative information on intra-specific variation.

The three most recent global forest resource assessments of FAO have dealt with the species level in different ways, by assessing endangered or threatened species, number of native tree species and the tree species composition of the growing stock, respectively ([FAO, 2001a, 2006, 2010a](#)). It should be noted that such parameters in themselves are of limited value as indicators of genetic diversity. For parameters to be useful as indicators they must not only be *quantified* and available in time series, but also *qualified in a relevant context* (see [FAO, 2001a](#)). A general problem is, for example, the apparent discrepancy between a seemingly well-known number of endangered species and much more uncertainty about the total number of species.

There are probably at least 60,000 tree species on Earth ([Grandtner, 2006](#)) and perhaps up to 100,000 ([Oldfield et al., 1998](#), cf. also [Petit and Hampe, 2006](#)). How many of these species are used by humans, or how many may become useful to human societies in the future remains an open question ([Dawson et al., 2014](#), this issue). Some 2500–3500 tree species have been registered as forestry or agroforestry species ([Burley and von Carlowitz, 1984](#); [Simons and Leakey, 2004](#)). Many of them are used largely in their wild state with relatively few brought into cultivation. Even fewer of them have ever been tested for population-level performance across different environments and very little is known about their genetic variation at any level; even their geographic distributions are often poorly documented ([Feeley and Silman, 2011](#)). In addition, many of them are considered threatened. The International Panel on Climate Change (IPCC) estimates that 20–30% of plant and animal species will be at risk of extinction if temperatures climb more than 1.5 to 2.5 °C ([IPCC, 2007](#), cf. also [Ruhl, 2008](#)). However, by the number of species alone, designing surveys to reveal intra-specific variation is obviously not an easy task.

The most recent global survey on forest genetic resources has been prepared in connection with the preparation of the State of the World's Forest Genetic Resources ([FAO, 2010b, 2014](#)). The Guidelines for the preparation of Country Reports for the State of the World's Forest Genetic Resources Report ([FAO, 2010b](#)) include an Annex 2, which consists of table templates to assist the organization and presentation of information. We compared the set of indicators in our [Table 2](#) (cf. also [Table 5](#), later) with these templates to evaluate the degree to which data would have been collected to inform the indicators if all of the templates were completed in the Annex 2 of [FAO \(2010b\)](#). Most of the requested data must be considered as input to response indicators, while one table can be seen as providing a state/pressure indicator. This is a table based on information requested on tree and other woody forest species considered to be threatened in all or part of their range from a genetic conservation perspective [Table 7 in Annex 2 of the Guidelines document ([FAO, 2010b](#))]. This set of information is relevant for the present review, because it can provide a

set of verifiable indicators likely to be associated with the state indicators on species distribution and genetic diversity in Table 2 (cf. also Table 5: Trends in species and population distribution pattern of selected species).

None of the table templates required genetic data that could show trends over time, for example population genetic parameters that could indicate gene flow trends, or quantitative trait variances that could indicate trends in the potential for adaptation. There may be several reasons for the low requirement for information that could inform state indicators instead of response indicators. Among them, the fact that no state indicator for genetic resources has been widely accepted and adopted, at any scale, is not a trivial problem. Furthermore, response indicators are much more easily understood and reported on, especially by non-geneticists. Few state indicators of tree genetic diversity can be fully addressed within the boundaries of one country, and this may also have contributed to the lack of information reported on such indicators.

We examined the completed Country Reports (cf. above) to determine how many countries attempted to complete the only table (number 7 in Annex 2, FAO, 2010b) that would inform a state/pressure indicator, and the amount of information that was provided. This information is summarized in Table 4.

Among the 84 Country Reports that we examined, 30 (36%) included information on at least one of the five parameter columns (Table 4). Only seven countries reported on all of them, four of which were in Europe. The two most informative columns in the table: *Area (ha) of species' natural distribution in your country if known* and *Average number of trees per hectare, if known* were least often completed (11 and 7 countries respectively) and the two columns with the highest response rate were those with the least inherent information value from the perspective of tree genetic diversity.

None of the Country Reports from South or Central America included the table from Annex 2 in FAO (2010b) with species distribution and threat information, but two of them reported on levels of genetic diversity. Two of the three North American reports included information about levels of genetic diversity for important tree species, but only one included the table. Genetic diversity parameters for key species were also reported by two Asian countries and two European countries.

The general lack of state/pressure type information that was requested from the countries emphasizes the need to focus more on identifying practical informative indicators that could be used to gather information in subsequent reporting cycles. The fact that a few countries did report on genetic parameters indicates that it is becoming increasingly feasible to do so. However, there must be a

standardized approach in order to achieve statistically interpretable results.

In summary, reasons for the overall scarcity of reported results for genetic indicators include difficulty, real or perceived, in measurement and interpretation, disagreement among experts on the minimal set of indicators required in order to provide useful information, lack of resources to add additional variables to the standard forest inventory data collection procedures, and possibly a lack of understanding among forest management practitioners about the relevance of genetic resources to forest sustainability. The challenge is thus to provide meaningful indicators that can be agreed upon and implemented in practice.

In the forestry sector, considerable theoretical progress in identifying relevant state indicators has been made over the past 20 years (Namkoong et al., 1996, 2002; McKinnel, 2002; Bariteau, 2003; Aravanopoulos, 2011) and much scientific attention has been paid to evolutionary and adaptive processes (e.g. Eriksson et al., 1993; Namkoong et al., 2002; Le Corre and Kremer, 2003, 2012) as a basis. However, a general application and scaling-up of the verifiers proposed by Namkoong et al. (2002) have not yet been feasible due to the difficulties summarized above.

4. What are meaningful and realistic indicators of tree genetic diversity?

4.1. Proposed operational indicators

Any relevant set of indicators for trends in genetic diversity must include components at different scales (local/landscape/national/regional/global), involving the amount of diversity and how it is distributed in space. There is a need to identify genetically appropriate indicators and, at the same time, not to inflate the already large number of indicators that exist at global and regional scales.

The State–Pressure–Benefit–Response (S–P–B–R) loop developed by UNEP/CBD/AHTEG (2011a,b) and Sparks et al. (2011) provides a well-considered and appropriate framework to ensure that the suggested set of indicators meet the requirements of being scientifically sound, realistic, and policy relevant; and the framework has been adopted for implementation by BIP, 2013. The identification of indicators of tree genetic diversity should therefore preferably take place within such a framework and result in a set of S–P–B–R indicators.

In Table 5 we list what we consider to be relevant operational indicators and their type (state, pressure, benefit, response) at dif-

Table 4
Summary of responses by region to the request for information that could inform a state indicator for forest genetic resources, in Table 7 of Annex 2 of the Guidelines (FAO, 2010b) for the preparation of Country Reports for the State of the World's Forest Genetic Resources (List of tree and other woody forest species considered to be threatened in all or part of their range from a genetic conservation perspective).

Region	Number of countries reporting	Number of countries that attempted Table 7 of Annex 2 in FAO (2010b)	Number of countries that provided information on each of the 5 parameter columns in Table 7 of Annex 2 in FAO (2010b)				
			Area (ha) of species' natural distribution in your country if known	Average number of trees per hectare, if known	Proportion of species' natural distribution that is in your country	Distribution in the country: widespread (W), rare (R), or local (L)	Type of threat (Code)
Sub Saharan Africa	26	7	2	1	2	6	7
Asia/Pacific	16	6	1	1	6	6	6
Central Asia	4	4	2	1	1	4	4
Europe	17	11	5	4	8	9	11
South and Central America	9	0	0	0	0	0	0
North America	3	1	0	0	1	1	1
North Africa/Near East	9	1	1	0	0	1	1
Total	84	30	11	7	18	27	30

Table 5

Types of possible operational indicators under the headline indicator “trends in genetic diversity (adaptive potential) of tree species”. Verifiers are presented in detail. The primary scale of measurement is given (see text for further information).

Operational indicator	Verifiable indicator	Verifier (direct or proxy)	Primary scale of measurement	
<i>State–Pressure</i>				
1. Trends in species and population distribution pattern of selected species	1. Number of species with known distribution for which allelic diversity is declining	1. Number of species with known distribution for which distribution is declining	Global/ regional/ national	
	2. Natural distribution range	2. Geographic and climatic range		
2. Trends in population condition	3. Distributional pattern within the natural distribution range where appropriate	3. Geographic, climatic and eco-geographic distribution of populations	Local	
	4. Representation within the natural range	4. No. of populations relative to their potential genecological distribution		
	5. No. of populations, their area and density (abundance)	5. Area and density of populations		
	6. Demographic condition of selected populations (diversity in adaptive traits/genes)	6. Demographic parameters and reproductive fitness		
	7. Genetic condition of selected populations (population genetic structure where appropriate)	6.1. Age/size class distribution		6.1. Age/size class distribution
		6.2. Number of reproducing trees		6.2. Number of reproducing trees
		6.3. Abundance of regeneration		6.3. Abundance of regeneration
		6.4. Environmental heterogeneity		6.4. Environmental heterogeneity
		6.5. Number of filled seeds		6.5. Number of filled seeds
	7. Genetic condition of selected populations (population genetic structure where appropriate)	6.6. Percentage of germination		6.6. Percentage of germination
7. Genetic parameters		7. Genetic parameters		
7.1. Effective population size		7.1. Effective population size		
7.2. Allelic richness		7.2. Allelic richness		
7.3. Outcrossing/inbreeding rate		7.3. Outcrossing/inbreeding rate		
3. Trends in plantation performance of selected species	8. Hectares planted by species/provenance either locally or as an exotic	8. Hectares planted by species/provenance either locally or as an exotic	Local/ national/ regional/ global	
	9. Profit from breeding vs. loss from ill-adapted plantations	9.1. Seed source performance (growth and survival) 9.2. Realized genetic gain and profit		
<i>Benefit</i>				
4. Trends in knowledge of genetic diversity of species	10. Increase in number of species that are described for which distribution and/or genetic parameters are known (and/or surrogates, e.g., traditional knowledge)	10. Increase in number of species that are described for which distribution and/or genetic parameters are known	Global/ regional/ national/local	
	11. No. of species with mapped genecological variation	11. Increase in number of articles on genetic diversity by species		
	12. Among population genetic diversity (of selected species)	11.1. No. of species with mapped genecological variation 12. Parameters of genetic differentiation among populations		
5. Trends in education and awareness	13. The change in number of tree geneticists and tree breeders	13. Number of university courses/ training courses offered in forest genetics-related subjects	National/ regional/ global	
	14. Existence of Forest Genetic Resource (FGR) networks	14. FGR networks (function/operation)		
	15. Consideration of tree genetic diversity in NFIs and NFPs	15. Mention/assessment of genetic diversity in NFIs and/or NFPs		
6. Trends in sustainable use of tree genetic resources	16. Number of tree species for which regulation of use of forest reproductive material exist	16. Number of tree species for which regulation of use of forest reproductive material exist	National/ regional/ global	
	17. Number and type of improved seed sources traded/exchanged (status of genetic improvement)	17. Number and type of improved seed sources traded/exchanged (Use also verifier 9.1 to characterise type of source)		
	18. Guidelines/regulations for matching seed source and planting site	18.1. Certification scheme in place 18.2. Use of adapted seed sources		
	19. Guidelines/regulations for composition and harvest of seed sources (number of mother trees)	19. Use of diverse seed sources		
7. Trends in genetic conservation	20. Number of tree species directly targeted in conservation programs	20. Number of tree species directly targeted in conservation programs	National/ regional/ global	
	21. Conservation action taken for species/ populations at risk (<i>in situ</i> and <i>ex situ</i>)	21.1. Existence of a national gene conservation strategy/program 21.2. Number and area of conservation units		

ferent geographic levels (global, regional/national and local) under the headline indicator *trends in genetic diversity of tree species*. Our table is not necessarily exhaustive, but proposes a fairly complete set of indicators and has been made in congruence with Table 2. However, no separate pressure indicators are identified. Pressure indicators of genetic diversity are intrinsically linked with state indicators and the identification of the impact of any kind of pressure will have to rely on the knowledge of the state. Response indi-

cators are referred to as response–benefit, because the rationale for a response is typically based on benefit.

In Table 5 we subdivide the headline indicator *trends in genetic diversity of tree species* into seven operational indicators. These are appraised based on 21 verifiable indicators using a total of 34 verifiers. Genetic diversity indicators that are proposed in order to assess the adaptive potential of forest tree species from the global to the local level present different characteristics, such as indicator

classification (state, pressure, benefit, response), reference level (global, regional, national, local), type of work needed (field, lab, web-based search, etc.), feasibility and type of expertise (direct measurement, or based on experimental analysis), level of informativeness, and cost. Each operational indicator is exemplified by verifiable indicators which in turn are assessed by a number of direct or proxy verifiers (verifiable measures). Therefore the practicality and potential prioritization of operational and verifiable indicators can be evaluated based on the verifiers needed for their assessment. The practicality of evaluating a verifier depends on the amount of work, time and costs, which, in turn, depend on the level of readily available and accessible knowledge associated with each verifier.

For the purposes of facilitating discussion and implementation, the seven operational indicators proposed in Table 5 can be further aggregated by type into four major operational indicator lines addressing the entire S–P–B–R framework, each of which is discussed further below:

- Trends in species and population distribution and diversity patterns for selected species, No. 1 and 2 in Table 5 (S, P).
- Trends in plantation performance of selected species, No. 3 in Table 5 (B).
- Trends in knowledge of genetic diversity of species and in education and awareness, No. 4 and 5 in Table 5 (R, B).
- Trends in management (sustainable use and conservation) of tree genetic resources, No. 6 and 7 in Table 5 (R, B).

4.2. Aggregated indicator 1: Trends in species and population distribution and diversity patterns for selected species

In Table 5, this major S–P indicator area is divided into two operational indicators, one each at the species and population level. The five verifiable indicators associated with the operational indicator *trends in species and population distribution pattern of selected species* cover global, regional and national reference levels (Table 5). These can be assessed by five highly informative verifiers in a straightforward manner at least for species where some background level of scientific knowledge exists (Table 5). This assessment can likely be carried out by using web-based means and databases, or national archives. However, for species where relevant information is not available, assessing this indicator will be a time consuming and cumbersome process.

A comparison of the past and present genecological distribution of selected species is a realistic way to assess intra-specific variation trends, thus it provides a state indicator of tree genetic diversity. Moreover, such a comparison also permits an analysis of the causes of anticipated loss, thereby revealing relevant pressures.

The genecological approach addresses genetic diversity at the regional scale where species' distributions are defined (from entire continents down to national and subnational levels). The perception of tree species consisting of a series of locally differentiated populations has been supported by numerous studies (cf. e.g., Rogers and Ledig, 1996). It has stimulated the development of experimental methods since the 18th century based on common gardens, i.e. planting trees of different origins within the same environment, so that the genetic component of phenotypic variation is revealed. The high level of differentiation among populations observed in adaptive genetic diversity, especially for growth capacity, largely inspired the development of forest genetics in the 20th century (Bariteau, 2003).

The ability to disperse genes over long distances by pollen or seed is a common feature of many tree species (Smouse and Sork, 2004) and this has a homogenizing effect, reducing differentiation due to divergent natural selection (Kremer et al., 2012). Differentiation at the local scale is therefore only expected to occur if

selective forces are strong over small distances (Eriksson et al., 2007). Thus, in the presence of moderate ecological gradients, the adaptive genetic differentiation within a species is anticipated to be manifested at a regional rather than a local level unless in the presence of strong barriers against gene flow at a local level (cf. e.g., Gaudal et al., 1997). The empirical evidence for the presence of adaptation is substantial in tree species. Provenance and common garden tests over the last century have provided ample evidence of adaptation on a regional scale and clinal patterns in species with continuous distribution across ecological gradients, even in the presence of substantial gene flow (Alberto et al., 2013). Most published studies are from temperate and boreal forests, but several studies in tropical tree species have identified similar levels of adaptation (Finkeldey and Hattemer, 2007; Ræbild et al., 2011). The genecological concept therefore builds on an expectation that genetic differentiation in adaptive traits will reflect the variation in ecological conditions at a regional level – at least as long as the species in question has a fairly continuous distribution containing viable populations. The genecological zonation approach thus provides a framework for predicting patterns of genetic variation in traits of adaptive significance between populations sampled range-wide. As the approach is based on the expectation that genetic patterns are generated from the balance between gene flow and selection, it will be less relevant for species that occur predominantly in small isolated populations where drift and inbreeding may have played a prominent role in developing genetic patterns. This limitation can include species with recent rapid geographic expansion or species subject to a recent hybridisation with native or introduced species.

Factors such as selection, migration and habitat range may affect species diversity and genetic diversity in the same direction (Vellend and Geber, 2006). However, the links between genetic diversity, species diversity, composition of communities and distribution are far from straightforward (e.g., Alonso et al., 2006). For example, restricted habitat and distribution often lead to low species diversity in communities (islands for example), but responses in terms of genetic diversity can vary widely. For instance, the California endemic *Pinus torreyana* (Ledig and Conkle, 1983) is genetically narrow (“depauperate”), but *Cedrus brevifolia* (Eliades et al., 2011), which has a distribution limited to a small area of Cyprus, is one of the most diverse conifers. Conversely, widely distributed species such as the Mediterranean *Pinus pinea* (Vendramin et al., 2008) and the North American *Pinus resinosa* (Echt et al., 1998; Mosseler, 1991, 1992; Allendorf et al., 1982) are genetically depauperate species. Bottleneck-related evolutionary factors may explain such discrepancies (e.g., Fady and Conord, 2010).

Although far from widespread (e.g., Feeley and Silman, 2011), data for a number of tree species enabling such genecological analyses are currently made available by the scientific community (such as EUFORGEN, 2013, MAPFORGEN and VECEA, cf. Bohn et al., 2002/3, 2007; Lillesø et al., 2005; Kindt et al., 2005, 2007a,b, 2011a,b,c,d; Mucina and Rutherford, 2006; Friis et al., 2010; Lillesø et al., 2011a; van Breugel et al., 2011a,b). Further work in this direction is laborious and complex, but significant progress can be made if for example it is dealt with by a network of national and international institutions that will jointly be responsible for assessment and evaluation.

Assessing indicators at the population level will likely be more resource demanding than the other levels, requiring commitment of significant resources at national and regional levels. Current work aimed at the development of genetic monitoring methods for genetic conservation units of European forest trees promises to be a valuable model (Aravanopoulos et al., 2014).

The local level is addressed by the operational indicator *trends in population condition* and two verifiable indicators pertaining to demographic and genetic verifiers (Table 5) are suggested. In this

case, both demographic and genetic parameters, 11 in total, are needed for evaluating population condition. Population demography, as well as fitness, can be assessed by simple field estimations and basic experiments in a straightforward manner. Therefore, besides demographic conditions, two important parameters at the local population level, selection and genetic diversity (the latter at an indirect level), can be assessed (Aravanopoulos, 2011; Konnert et al., 2011).

The direct estimation of population genetic parameters, including genetic drift and erosion, and gene flow and population structure, can be undertaken with molecular genetic markers, but this involves significant costs and particular expertise. Although the costs of molecular genotyping are decreasingly rapidly compared to the costs of phenotyping, the latter remains the main or only option in many countries.

With sound experimental design and proper care of field studies, phenotypic data from field trials can yield valuable information about genetic diversity and population structure with respect to adaptive traits, but as such studies are generally more expensive now than molecular analyses, it is not feasible to monitor change over time based on such studies only.

The assessment of demography and the partial assessment of genetic status at this level will provide some indication of population condition and may on a temporal scale show some underlying trends. However, it is in combination with the full assessment of the genetic status, through the genetic parameters indicated, that a complete evaluation of population condition at the local level may be achieved.

The use of already existing information regarding the demographic and genetic conditions of a population is not advisable to inform current status, unless this information is recent (less than a decade old). Otherwise, climatic change and anthropogenic influence may deem the literature outdated. On the other hand, older data are indispensable for establishing temporal comparisons needed to identify trends in population condition.

4.3. Aggregated indicator 2: Trends in plantation performance of selected species

Trees in plantations and on-farm will be one of the major assets of a future global and local economy relying on renewable resources. Through appropriate management of genetic resources (which constitute an indicator area of its own), the benefits of tree planting can be increased many fold. A valuation of this effort in terms of the extent and development of selected tree planting activities and the use of relevant reproductive material can provide a direct indicator of benefit. It may also serve as a verifier for the management of the genetic resource itself (i.e. response), but it is important to emphasize the level of benefit that can be achieved.

The Planted Forest Programme of FAO (FAO, Planted Forest Programme, 2013) has compiled and analyzed information on planted forests for more than a decade. In addition, an increasing amount of information on trees outside forests is becoming available (Zomer et al., 2009). The relative contribution of planted forests to the global production of wood serves as a general indicator of the importance of tree plantations. In 2005, forest plantations covered some 260 million ha or 7% of the global forest area, but produced 1.2 billion m³ of industrial round wood or about two thirds of the total global round wood production (Evans, 2009). By 2030 the production from plantations may surpass 2 billion m³ of industrial round wood. Given the increasing importance of planted forests, information on trends in genetic diversity, deployment and productivity of a selection of planted tree species could be a feasible indicator of benefit.

The benefit of genetic diversity as a resource is directly expressed in the value of tree breeding. The profitability of breed-

ing is well established (e.g., Daniels, 1984; Foster et al., 1995; McKeand et al., 2006; Rosvall, 2011; Willan, 1988). Through a fairly simple process it is possible to achieve 35–80% gain with very high returns of investment (see Foster et al., 1995). The basic requirement is of course the availability of genetic diversity. With the increasing focus on the need for a so-called 'green' bio-based economy, there would seem to be a dire need to bring focus back on the societal benefits of tree breeding (Graudal and Kjær, 1999), not only to increase production but also to alleviate the negative impact of harvesting natural forest to reduce illegal exploitation of even some conservation areas (e.g., WWF, 2012).

The proposed operational benefit indicator is thus *trends in plantation performance of selected species*, which is associated with two verifiable indicators and three verifiers. The only verifier that would be simple to use "hectares planted by species/provenance either locally or as an exotic" provides only partial assessment. The two other verifiers are more complicated to measure. These are "seed source performance: growth and survival" which can be assessed experimentally, and "realized genetic gain and profit" which can be assessed by employing a quantitative genetics approach in a suitable sample of genetic entries.

Indicators of the more subtle benefits related to ecosystem services and the management of natural ecosystems (e.g., natural forest management and restoration) still require development. There is a clear need to link genetic variability and ecosystem services, but we should also be aware of the dual nature of genetic diversity, as on the one hand a necessary precondition for future evolution of local populations, entire species and ecosystems, and on the other hand a service provider (e.g., for breeding programs). In both cases the integration of genetic diversity into climate change adaptation planning is important (Alfaro et al., 2014, this issue). Additional work in this area is required.

4.4. Aggregated indicator 3: Trends in knowledge of genetic diversity of species and in education and awareness

Knowledge, education and communication are closely linked. Scientific knowledge can be gathered from the literature, whereas traditional knowledge can be more difficult to capture. The state of education may to some extent be available from national statistics and may be collected through national surveys. Assessment of trends will probably have to rely on special studies. Knowledge on intra-specific variation can be immediately connected to the two indicator areas discussed above, *trends in species and population distribution patterns and condition* and *trends in plantation performance*.

Two combined response and benefit operational indicators are related to knowledge and capacity building, with six verifiable indicators listed for the global, regional and national levels, while one *trends in knowledge of genetic diversity of species* is also proposed for assessment at the local level (Table 5). In total, there are seven associated verifiers and all except one ("parameters of genetic differentiation among populations", Table 5) can be evaluated based on background information such as National Forest Inventories (NFIs) and National Forest Programs (NFPs), or based on database searches. The estimation of verifier "parameters of genetic differentiation among populations" would require the use of molecular genetic markers and/or the evaluation of suitable field trials. Overall the evaluation of the operational indicators is, in principle, straightforward, even if the operational indicator *trends in knowledge of genetic diversity of species* is assessed based on three out of four dedicated verifiers.

The recent rapid development of molecular marker techniques (Allendorf et al., 2010) has greatly facilitated the identification of state indicators at the level of the management unit of identified priority species (Aravanopoulos, 2011; Funk et al., 2012; Geburek

et al., 2010; Hansen et al., 2012; Konnert et al., 2011; Laikre et al., 2008; Luikart et al., 2010; Schwartz et al., 2007; Stetz et al., 2011). Such techniques are available at the scientific level and within reach at a practical level, at least where facilities are available. However, in practice availability depends on access to resources and facilities which varies enormously among countries and world regions. In Europe, work by the European Forest Genetic Resources Network (EUFORGEN) has reached a point where implementation of molecular based techniques is likely to begin within a few years (Aravanopoulos et al., 2014).

While the increasing utility and the decreasing costs of molecular techniques hold great promise for providing efficient means for monitoring genetic diversity, it is imperative that the basic importance of taxonomy, ecology and field testing are not neglected. The diminishing priority of sustainable forest management in the national policies of some countries (Wijewardana, 2006), loss of competence in taxonomy (Drew, 2011; Hoagland, 1996; Kim and Byrne, 2006) and erosion of applied programs of genetic resource management (Graudal and Kjær, 1999; Graudal and Lillesø, 2007) are therefore of great concern. There seems to be an on-going world-wide trend of loss of practical knowledge and ability in tree species identification, tree seed handling, tree breeding and tree genetic resource conservation management (Graudal and Lillesø, 2007), which will be an impediment for the implementation of any program to use and conserve tree genetic diversity. Indicators to monitor this area of response policy would therefore be highly relevant and can be measured through national surveys.

4.5. Aggregated indicator 4: Trends in management (sustainable use and conservation) of tree genetic resources

Management responses can be measured by the extent of physical management and conservation activities in the field, and by the integration of response measures in policy, planning and the implementation of programs, including in legislation. Some of these elements are, in principle, easily evaluated by quantification of breeding and gene conservation activities at the national level and are already available and being used in some geographical areas.

Measuring legislation or regulation responses is probably more difficult but one approach would be for example to quantify the adoption of certification schemes for distribution and exchange of reproductive material. Schemes exist for some areas, but it is important to validate whether such schemes are relevant for the purpose they are intended before they are used as a positive measure of action (Lillesø et al., 2011b).

Two combined response and benefit operational indicators are related to the use of tree genetic diversity and six verifiable indicators are listed for the global, regional and national levels (Table 5). There are nine associated verifiers and all except one (“seed source performance”, Table 5) can in principle – as for verifiers of knowledge generation and capacity building referred to above – be evaluated based on background information (NFIs and NFPs), or based on database searches, although some (“use of adapted seed sources” and “use of diverse seed source”) likely will be rather poorly covered. The estimation of verifier “seed source performance” would require a seed testing experiment (which could already have been undertaken as part of the reproductive fitness assessment of indicator “trends in population condition”). Again, the evaluation of these operational indicators is, in principle, straightforward, although assessment of operational indicator trends in sustainable use of tree genetic resources may be based only on three out of five dedicated verifiers (Table 5). All four response-benefit indicators can be assessed without the need of an experimental approach, two fully and the other two based on an average of around 75% of the suggested verifiers.

Table 5 can be seen as providing indicators for the management of reproductive material coupled with breeding programs, and for the implementation of specific gene conservation programs. This is similar to the current reporting by Forest Europe et al. (2011). It is however important to connect such reporting with a relevant genealogical baseline.

Our suggested genealogical approach is similar to that used by the EU as part of the Marine Strategy Framework Directive (European Commission, 2011). A comparison between these widely different habitats is useful because some marine organisms and trees have similar life history traits such as long life span, high dispersal ability and large distribution areas. Like marine organisms, forest trees provide ecosystem services of disproportionately large importance relative to their distribution and frequency. Monitoring marine genetic resources is mandated by legislation in the form of an EU Commission decision. The feasibility of applying legislative measures in support of monitoring other types of biodiversity, including forest tree genetic diversity, should be considered.

In the forestry sector, such an approach could be combined with the regulation of forest reproductive material (FRM). Statistics on the use of forest reproductive material (e.g., seed sources) over time would not be enough to assess trends in tree genetic diversity. However, when statistics exist on the use and trade of FRM, and when provenances are delineated and their diversity is estimated, such an indicator may be useful. Regions of provenances and the mandatory use of passport data on geographic origin should therefore be established where they do not exist and statistics on FRM collection and trade should be compiled (see also Koskela et al., 2014, this issue).

The management of natural forests constitutes a particularly complex area for maintaining genetic diversity (Thomson, 2001) because the management objective, whether for conservation or for production, ultimately depends on the genetic diversity present. The notion ‘conservation through use’ (Graudal et al., 1997) is applied when forest management deliberately takes care also of genetic diversity. In this context, we have not tried to identify a particular indicator but would consider this covered by the overall monitoring of trends in species and population distribution and diversity patterns.

4.6. Toward scientifically sound, realistic and implementable tree genetic diversity indicators

In general, five of the seven operational indicators suggested above can readily be assessed, provided that some level of background information is available. The appropriate level of information is likely available at least for selected key species of ecological and/or economic importance and for a number of endangered flagship species, where forestry operations and/or conservation actions have generated considerable knowledge. These five indicators can be prioritized for the assessment of the headline indicator “trends in genetic diversity of tree species” at the global, regional and national levels; however all indicators should be employed for a comprehensive evaluation at the local level.

The vast array of indicators that have been proposed for monitoring genetic diversity can be distilled into the set of four aggregated indicator areas that cover the S–P–B–R spectrum of UNEP/CBD/AHTEG (2011a,b) and Sparks et al. (2011). Table 6 gives a brief characterization of the proposed set of indicators. Our “diversity–productivity–knowledge–management” (DPKM) typology is thus a set of four indicators that derives mostly from the genealogical approach to genetic diversity and can be applied at multiple scales, from global to local. The typology is intended to emphasize the available potential for development or change in managing the evolutionary potential of trees within and outside forests.

Table 6

The “diversity–productivity–knowledge–management” (DPKM) typology of tree genetic diversity indicators. A brief characterization of a proposed set of four operational indicator lines, that can be used for an overall assessment of the headline indicator “trends in genetic diversity of tree species”. The four operational indicator lines follow the S–P–B–R framework. Implications emphasize the potential for development.

Operational indicator line	Implications	Possible primary sources of data and information
Trends in species and population distribution and diversity patterns for selected species	The <i>state</i> of the genetic <i>diversity</i> of trees: what is really happening to the resource?	International, regional and national data bases, FAO Forest Resources Assessment (FRA)
Trends in plantation performance of selected species	The <i>productivity</i> of the genetic resource of trees in current use; also reflecting the possible potential of mobilizing the resource further	NFIs, FAO Planted Forest Programme, FAO FRA
Trends in knowledge of genetic diversity of species and in education and awareness	Current <i>knowledge</i> and potential capacity for development of the genetic resource	Scientific literature, various databases and national institutions
Trends in management (sustainable use and conservation) of tree genetic resources	Current <i>management</i> of the genetic resource: how well are we actually doing?	National and international institutions and networks

5. Conclusions

Because trends in genetic diversity (and therefore long term adaptive potential) need to be known before the impact of any type of pressure can be assessed, providing a relevant state indicator represents the most crucial step of the assessment procedure. Response, pressure and benefit indicators cannot and should not be used independently of state indicators. Drawing from quantitative and population genetics, substantial theoretical progress has been made over the past 20 years for identifying relevant state indicators of tree genetic diversity. However, these scientifically sound indicators have so far proven difficult to apply in practice. Pressure indicators of genetic diversity are intrinsically linked with state indicators and have therefore in practice not been identified on their own. Benefit indicators for genetic diversity can only be implemented if a valuation of genetic diversity is available. Apart from the value of breeding, such valuation is rare (see also Dawson et al., 2014, this issue). Response indicators are generally much easier to define, because recognition and (even) quantification of research, education, breeding, conservation, and regulation actions and programs, are relatively straightforward.

The attempts of the forestry sector to use genetic diversity indicators in practice have therefore been limited to response indicators in general, which do not provide any real information on the status of the genetic resources of trees on the planet, apart from assessments of threat at the species level provided by red lists of threatened taxa.

It is important to emphasize the link between species diversity and genetic diversity, making species level indicators relevant to genetic diversity. However, the correlation is true only up to a certain point. Thus, to effectively conserve the genetic diversity of a species, this diversity should be known. For most species, though, knowledge of genetic variation is minimal, pointing to the central dilemma of gene resource conservation: a recognized need for conservation without knowing exactly what to conserve. Knowledge of genetic variation will therefore, to a large extent, have to be derived from such surrogates as the species' ecological diversity (e.g. habitat diversity, diversity of ecological requirements).

Although considered unrealistic 20 years ago, a number of state indicators can now be proposed for (immediate) implementation because of scientific advances such as in geographical information systems, high throughput molecular genotyping techniques and the ability to handle large amounts of data (e.g., presence/absence species data). Concurrently, ecological monitoring and sustainable management (including management for genetic resources) have made significant progress.

The theoretical basis of the *diversity–productivity–knowledge–management* (DPKM) indicator typology we propose is the “gene-cological” approach, where three factors are the major forces of evolution at the ecosystem/population micro-scale: natural selection, genetic drift, and gene flow. The effects of natural selection

can lead to differentiation associated with local adaptation, while genetic drift can lead to differentiation associated with stochastic changes and genetic erosion, both being modulated by the action of gene flow that can lead to genetic homogenization.

The DPKM set can be applied on appropriate groups of tree species, in the wild and under cultivation, representing different regions and different climates, present as well as projected future. It is flexible enough to accommodate additional knowledge as it becomes available and, in principle, easily and cost effectively implementable by managers.

The DPKM set has the potential to provide a realistic picture of the state, trends and potentials of the world's tree genetic resources. Efficient implementation strategies for management worldwide include establishing links with FRM rules and regulations, and sustainable management certification schemes. It is probably realistic to assume that the wise use of genetic resources is one of the real options available to support sustainable growth. Using the DPKM typology is an attempt to underline this potential. Although we are at a stage where a number of indicators can be proposed, some for immediate implementation, the implementation of genetic diversity indicators must be tested in different forest zones, and for different categories of species (autoecology).

The establishment of Sentinel Landscapes, a new initiative of the CGIAR Consortium Research Programme on Forests, Trees and Agroforestry (CGIAR CRP6, 2013), provides an opportunity for testing and applying these indicators. Sentinel Landscapes are located in Africa, Asia and Latin America, each one spanning national boundaries and including forest-to-farm and environmental gradients. They are intended to provide sites for long term research and monitoring and would be one way forward for exploring regional down to management unit level indicator value. The possibility of applying such work as part of the ongoing effort to identify essential biodiversity variables (Pereira et al., 2013) could be explored. Further, data provided in World Reports such as the Forest Resources Assessment of FAO could be used to indirectly assess genetic diversity of trees at a global level, its status and the threats to it (S and P indicators).

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tents, structure and language were provided by two anonymous reviewers.

Appendix A. Abbreviations and acronyms

ABS	Access and Benefit Sharing
ACT	Amazon Cooperation Treaty
ACTO	Amazon Cooperation Treaty Organisation
AHTEG	Ad-hoc Technical Expert Group on Indicators for Biodiversity
ATO	African Timber Organisation
B	benefit (type of indicator)
BIP	Biodiversity Indicators Partnership
C&I	criteria and indicators
CABI	Commonwealth Agricultural Bureau International
CBD	Convention on Biological Diversity
CGIAR	Consultative Group on International Agricultural Research
CIFOR	Center for International Forestry Research
CILSS	Comité Inter-Etats pour la Lutte contre la Sécheresse au Sahel (Permanent Inter-State Committee for Drought Control in the Sahel)
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CMS	Convention on Migratory Species
CNR	Consiglio Nazionale delle Ricerche (Italian National Research Council)
COP	Conference of the Parties
CRP 6	Consortium Research Programme 6 of the CGIAR
D	driver (indicator)
Danida	Danish International Development Agency
DFSC	Danida Forest Seed Centre (now FLD)
DNA	Deoxyribonucleic Acid
DPKM	Diversity–Productivity–Knowledge–Management (indicator set)
EU	European Union
EUFORGEN	European Forest Genetic Resources Network
FAO	Food and Agriculture Organisation of the United Nations
FGR	Forest Genetic Resources
FLD	Forest & Landscape Denmark, University of Copenhagen
FRA	Forest Resources Assessment
FRM	Forest Reproductive Material
FSC	Forest Stewardship Council
FTA	Forest, Trees and Agroforestry
I	impact (indicator)
IBPGR	International Board for Plant Genetic Resources (now Bioversity International)
ICRAF	International Centre for Research in Agroforestry (now the acronym for World Agroforestry Centre)
ILRI	International Livestock Research Institute
INIA	Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (National Institute of Agrarian and Food Research and Technology), Spain
INRA	Institut National de la Recherche Agronomique (French National Institute for Agricultural Research)
IPCC	Intergovernmental Panel on Climate Change

IPGRI	International Plant Genetic Resources Institute (now Bioversity International)
ITTO	International Tropical Timber Organisation
IUCN	World Conservation Union (International Union for Conservation of Nature)
LAFORGEN	Latin America Forest Genetic Resources Network
MAPFORGEN	Atlas for the conservation of forest genetic resources, Bioversity International, INIA (Spain) and LAFORGEN
MDG	Millennium Development Goals
MEA	Millennium Ecosystem Assessment
NFI	National Forest Inventory
NFP	National Forest Program
OECD	Organisation for Economic Co-operation and Development
P	pressure (type of indicator)
PEFC	Programme for the Endorsement of Forest Certification (/Pan European Forest Certification)
R	Response (type of indicator)
REFORGEN	FAO worldwide information system on forest genetic resources
S	state (type of indicator)
SCBD	Secretariat of CBD
SEC	Staff Working Document European Commission
SLU	Swedish Agricultural University
S–P–B–R	State–Pressure–Benefit–Response (indicator framework)
UNCCD	United Nations Convention to Combat Desertification
UNECE	United Nations Economic Commission for Europe
UNEP	United Nations Environment Programme
UNFF	United Nations Forum on Forests
VECEA	Vegetation and Climate Change Eastern Africa
WCMC	World Conservation Monitoring Centre
WWF	World Wide Fund for Nature

Appendix B. Types of indicators and indicators relevant for tree genetic diversity

B.1. Types of indicators

Indicators must be scientifically sound, technically realistic for monitoring and relevant for defining a policy baseline. Policy relevance can vary across scales from global to the local forest plot level. Indicators can be used to measure the achievement of a target in different ways and, in the terminology used here, fall within one of four categories: state, pressure, response, and benefit (Sparks et al., 2011; UNEP/WCMC, 2011).

A state (S) indicator is a direct estimate of the status of a resource or a practice. When state indicators are assessed over regular time intervals, trends can be identified. An indicator can also indirectly track incidents or activities that pose a threat to a resource or a practice, e.g., deforestation, and then it is referred to as a pressure (P) indicator. When an indicator indirectly reflects an action towards improving the status of a resource or practice (whether by implementing a strategy or regulation, or by capacity building), it is referred to as a response (R) indicator. Most of the literature on indicators classically distinguishes among S, R and P

indicators in a coherent framework (e.g., Namkoong et al., 2002). Namkoong et al. (2002) present a conceptual model of the relationship between P, S and R indicators in the context of the response being that of biodiversity itself (ecosystem response, also called ecosystem process e.g., by Brown et al., 1997) rather than that of humans (societal response), i.e. different from the way the term response is now used within the framework of CBD.

More recently, benefit, understood here as the amount and change in benefit that humans derive from a resource or a practice, has been recognized as a valuable indicator for assessing biodiversity loss (e.g., Sparks et al., 2011; UNEP/WCMC, 2011). Benefit (B) indicators are intended to address value within an “ecosystem service” framework (MEA, 2005).

The pressure–state–response (P–S–R) framework was introduced by OECD (1993) and was gradually refined into the driver–pressure–state–impact–response (D–P–S–I–R) framework (Smeets and Weterings, 1999) that has been widely used in various forms. Impact (I) reflects the change of the state (and resulting changes on social and economic functions) caused by pressure. Benefit in the notion of Sparks et al. (2011) thus corresponds to impact. A driver (D) causes pressure, e.g., agricultural expansion leading to deforestation. Drivers are not considered separately by UNEP/CBD/AHTEG (2011a,b), but dealt with as part of pressures.

Sparks et al. (2011) argued that linking indicators into an integrated response–pressure–state–benefit framework (called the “R–P–S–B feedback loop”) would facilitate an understanding of the relationships between policy actions, anthropogenic threats, the status of biodiversity and the benefits that people derive from it, at global, regional, national and local scales. This framework is considered useful to guide decision making and for communication, particularly at national and local scales; it was introduced by UNEP for its Strategic Plan for Biodiversity 2011–2020 (UNEP/CBD/AHTEG, 2011a,b) and is now used by BIP (BIP, 2013).

B.2. Indicators relevant for tree genetic diversity

So far *tree genetic diversity* is not explicitly covered by any of the indicators currently reported in BIP (2013; Chenery et al., 2013), but the proposed set of operational indicators (UNEP/CBD/AHTEG, 2011a,b) and the flexibility of the framework provide the opportunity to include such coverage.

In this study, we refer to indicators of tree genetic diversity rather than to indicators of forest genetic resources. Forest genetic resources typically refer to the genetic variation of forest trees of present or potential value for humans. The importance of trees and other woody perennials outside forest is increasingly acknowledged (e.g. Zomer et al., 2009); therefore they are also considered here. The notion of potential value in a likely different future (Alfaro et al., 2014, this issue) implies that different species than the ones currently harvested and used will also benefit mankind. Thus, not only currently known important adaptive genes (genetic resources of present value), but the full spectrum of genetic diversity, is considered here. In reality, the resource cannot be distinguished from the diversity (Graudal et al., 1995). For the sake of simplicity, we therefore refer to “tree genetic diversity” as the area of interest of this study.

There is a close relationship between the presence of genetic diversity in fitness related traits and the ability of a species to adapt to new growth conditions or challenges caused by new pests or competition from other species (Aitken et al., 2008; Jump et al., 2009). The loss of adapted forests and trees is an issue of worldwide concern under global change, and the overall goal of indicators of tree genetic diversity must therefore be to identify trends in maintaining and enhancing *the adaptive (evolutionary) potential of tree species*. Thus indicators should be designed to monitor trends which reflect this target. This is crucially important for

the long term sustainability of the forestry and other tree-based sectors.

State indicators need to be designed for analyzing the status of genetic diversity of trees and how it changes over time and space. Species diversity has been found to be linked with genetic diversity (cf. Vellend and Geber, 2006; Vellend, 2006; Alonso et al., 2006), making species level indicators relevant for monitoring genetic diversity status, but the correlation has limitations. Particularly at large spatial scales in heterogeneous environments, species level indicators cannot be considered to be surrogates for genetic ones (Fady and Conord, 2010; Taberlet et al., 2012). With decreasing laboratory costs for molecular marker techniques, basic knowledge of genetic diversity has increased substantially over the last decades for many forest tree species and is likely to continue to do so (Allendorf et al., 2010). Usually, however, information on the assessment of S and P indicators of genetic diversity of trees must rely largely on surrogate measures, mostly species’ ecological requirements and biogeographic distributions (species auto- and gen-ecology, cf. Graudal et al., 1995, 1997).

Pressure (P) indicators must target the range and intensity of causes contributing to decline or loss of tree genetic diversity (and for which a response is needed). They are to a large extent linked with S indicators (demographic and genetic processes affecting the status of the genetic diversity of trees), although the natural and human-mediated causes for process alteration may not always be easily understood. R indicators for tree genetic diversity monitor the effects of policies and management strategies designed to prevent or reduce its loss.

Finally, B indicators quantify the benefits that humans derive from tree genetic diversity. While work on developing S, P and R indicators of tree genetic diversity has been going on for some time, little has been done on B indicators (Sparks et al., 2011). Although different methods are available to estimate the value of genetic resources (Sarr et al., 2008; Thorsen and Kjær, 2007; Goeschl and Swanson, 2002), few have been used (Bosselmann et al., 2008; Hein and Gatzweiler, 2006), so the value of genetic resources is mostly unknown (Elsasser, 2005).

Appendix C. Genetic diversity indicators considered as part of International Sustainable Forest Management Criteria and Indicator Processes

We have summarized these in Table C1. Although the list of indicators presented in Table C1 is impressive in its breadth and intentions, only a few have actually been measured and monitored (Chun, 2005; Rametsteiner, 2006; Wijewardana, 2006).

Among the 16 genetic diversity indicators listed in Table C1, six refer to the state of the resource while the other 10 correspond to a management or policy response. Taken together, only two state and four response indicators can be considered unique and non-overlapping among the different sets.

The two distinct state indicators are:

- Number and geographic distribution of forest associated species at risk of losing genetic variation and locally adapted genotypes (also, “Number of forest dependent species with reduced range”).
- Population levels of selected representative forest associated species to describe genetic diversity (also, “Population levels of key species across their range”).

The term population level is not well described in the quoted sources. It is supposed to reflect genetic diversity of forests and must therefore embrace variation among and within populations of a given species, but is somehow intended to go beyond the spe-

Table C1

Genetic diversity indicators associated with biodiversity-related criteria for major regional sustainable forest management monitoring processes. The formulation of the indicator in the text column is quoted from the source mentioned in the process column. Year refers to the date of the indicator version presented. Number is the original number of the indicator in the process. Type: classification of type of indicator (S: state, R: response).

Process, region and year initiated	Year	Number	Text (quoted from source)	Type
Montreal Process <i>Temperate and Boreal Forests</i> 1995 (Anon, 2009)	2007	1.3 a	Number and geographic distribution of forest associated species at risk of losing genetic variation and locally adapted genotypes	S
		1.3 b	Population levels of selected representative forest associated species to describe genetic diversity	S
		1.3 c	Status of on-site and off-site efforts focused on conservation of genetic diversity	R
Pan-European Forest Process (previously Helsinki Process) 1993 (Forest Europe et al., 2011)	2002	4.6	Area managed for conservation and utilization of forest tree genetic resources (<i>in situ</i> and <i>ex situ</i> gene conservation) and area managed for seed production	R
Tarapoto Proposal <i>Amazon Forest</i> 1995 (ACT, 1995)	1995	4.3	Measures for the conservation of genetic resources	R
The Near East Process <i>Near East</i> 1996 (FAO, 1999)	1996	2.9	Existence of the number of seed provenance	R
		2.10	Number of forest dependent species with reduced range	S
		2.11	Population levels of key species across their range	S
Dry Forests Asia Process <i>South & Central Asia</i> 1999 (FAO, 2001)	1999	3.6	Existence of mechanisms for the conservation of genetic resources	R
African Timber Organization <i>West and Central Africa</i> 1993 (Anon, 1998)	1994	IIA.1.3	In the area of harvesting, the standards are explicit on minimum number of large trees to be retained as seed producers (mother trees) per ha and species	R
The Dry-Zone Africa <i>North, East and Southern Africa</i> 1995 (Anon, 1999)	1999	2.9	Average number of provenances	R
		2.10	Number of forest dependent species with reduced range	S
		2.11	Population levels of key species across their range	S
		2.12	Management of genetic resources	R
International Tropical Timber Organization <i>Humid tropics</i> 1992 (Anon, 2005)	2005	5.5	Measures for <i>in situ</i> and/or <i>ex situ</i> conservation of genetic variation within commercial, endangered, rare and threatened species of forest flora and fauna	R
Lepaterique Process <i>Central America</i> (Anon, 1997)	1997	5.6	Number of species conserved <i>ex situ</i> (e.g., in seed banks)	R

cific species (cf. FAO, 2001). For practical use, the term would need to be better defined.

The four response indicators are:

- Status of on-site and off-site efforts focused on conservation of genetic diversity (also “area managed for...”, “mechanisms for...”, “measures for...”).
- Existence of the number of seed provenance (also “average number of...”).
- In the area of harvesting, the standards are explicit on minimum number of large trees to be retained as seed producers (mother trees) per hectare and species.
- Management of genetic resources.

In principle such indicators could have been part of the 2010 Biodiversity Indicators of CBD, but none of this kind were explicitly included (SCBD, 2006, 2010). However, if better defined they could be included and adopted in the framework proposed for 2011–2020 (cf. Table 2).

Forest Europe reported on the Criteria and Indicators set of the Pan-European Process (Forest Europe et al., 2011), which attempted to measure and report on genetic indicators. The areas managed for *ex situ* conservation and seed production were found to have increased during the reporting period (from 1990 to 2010). More than 450,000 hectares of forest were reported to be managed for *in situ* conservation, covering a total of 142 tree taxa, including species, sub-species and hybrids. The report noted that “there are significant gaps in the geographical representativeness of *in situ* gene conservation areas as compared to the distribution maps of European tree species”, and furthermore, that “wide coverage of areas for gene resources ensures the capacity of forest trees to adapt to climate change”. Overall the assessment showed positive trends. Although it is laudable that an assessment of genetic indicators was included in the report, it illustrates the weakness of reporting only on response indicators without measuring state indicators, because an increase in the area reported for *in situ* and *ex situ* conservation does not *per se* document improved conservation status of the forest genetic resource itself.

The indicators listed in Table C1 include only those that were specifically intended as indicators of genetic diversity (although some fall more closely into the species-level indicator category). There are other indicators that are not listed here, which measure biodiversity at the ecosystem and species levels, but could also be important for genetic diversity. For example, indicators relating to the extent of protected areas, forest cover and fragmentation, and to the degree of destructive harvest. In some cases these have been assessed more successfully than those indicators that are specific to genetic diversity. Population size and the degree of fragmentation are important indicators of loss of genetic diversity because they affect genetic drift.

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