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Current Opinion in Environmental Sustainability

Constraints and opportunities for tree diversity management along the forest transition curve to achieve multifunctional agriculture☆

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On-farm tree diversity patterns result from a social-ecological process shaped by different actors. Farmer preferences, tree-site matching, seed dispersal, tree domestication and delivery via nurseries all play important roles in forming these patterns. As part of a wider interest in tree cover transition curves that link agroforestation stages of landscapes to a preceding deforestation process, we here focus on 'tree diversity transition curves' i. as a conceptual framework to understand current processes and how shifts in drivers affect tree diversity and ii. to help identify constraints and opportunities for interventions. We provide some examples of current research efforts and make suggestions for databases and analyzes that are required to improve our understanding of tree diversity transitions. We explore drivers, consequences and entry points for tree diversity management to achieve multifunctional agriculture.

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Current Opinion in Environmental Sustainability 2014, **6**:54–60

This review comes from a themed issue on **Terrestrial systems**

Edited by **Cheikh Mbow**, **Henry Neufeldt**, **Peter Akong Minang, Eike Luedeling** and **Godwin Kowero**

Received 5 June 2013; Accepted 15 October 2013

http://dx.doi.org/10.1016/j.cosust.2013.10.009

Introduction

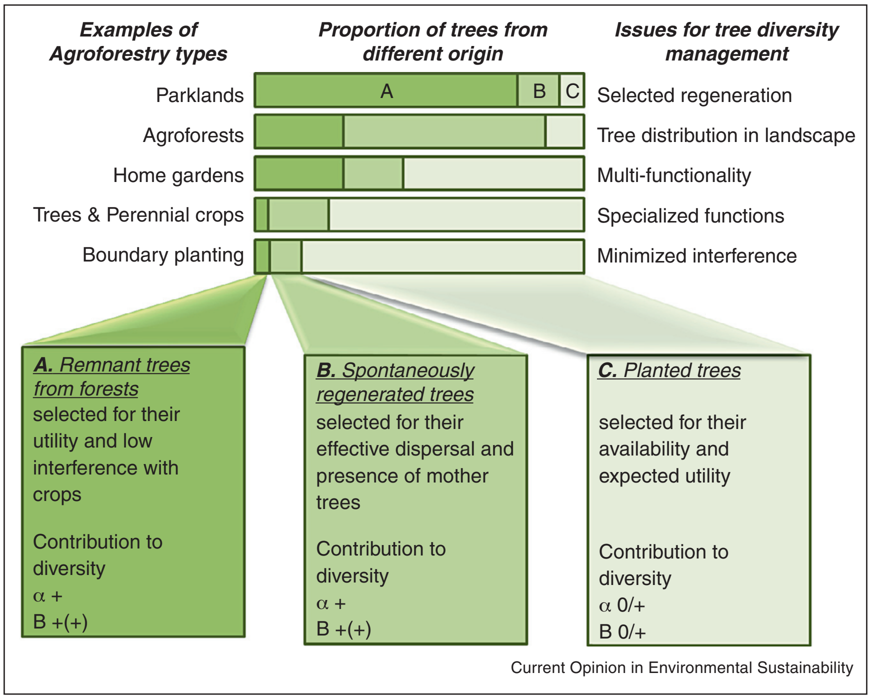
Trees on farms can result from three processes: (A) retention of trees that were present before farms were established, (B) tolerance (and protection) of natural tree regeneration after farms were established, or (C) active planting by farmers of selected trees in preferred locations. Many agricultural landscapes include trees derived from more than one of these processes (Figure 1). In this context we include as trees any woody perennial growing in agroforestry land use systems, or forest remnants. Typically after an initial period of deforestation, trees on farms are remnants of previous vegetation, followed by a gradual loss of trees of type A and B, ultimately leading up to a phase of deliberate tree establishment by farmers (type C. Figure 1). This sequence of processes has become known as the tree cover transition curve [1], a reinterpretation of the forest transition curve [2•]. The set of trees that ends up being present on farms depends greatly on the interaction of ecological and social-economic-cultural processes. We use the tree cover transition curve as a framework for understanding the determinants of tree diversity (in terms of species and functions) on farms, and to explore potential implications of changes in tree diversity for biodiversity conservation, provision of ecosystem services and human livelihoods.

The tree cover transition curve as a framework for tree diversity research

The tree cover transition curve is a conceptual framework that links agroforestation stages of landscapes to a preceding deforestation process [2•,3]. Tree cover transitions can be evaluated on the basis of biomass or carbon stocks, but also on the basis of tree species diversity. The transition typically starts with a gradual change in diversity (e.g. declining diversity and increase in evenness) of spontaneously established trees on farms after deforestation, which is often followed by recovery of tree diversity through agroforestation, driven mainly by active tree planting (Figure 2).

Tree diversity dynamics are determined by factors operating at different stages of tree growth, from tree establishment to reproduction, a process that normally involves several growing seasons (several years). Factors that influence tree diversity during this time can be natural or anthropogenic: including social, economic or cultural

Figure 1



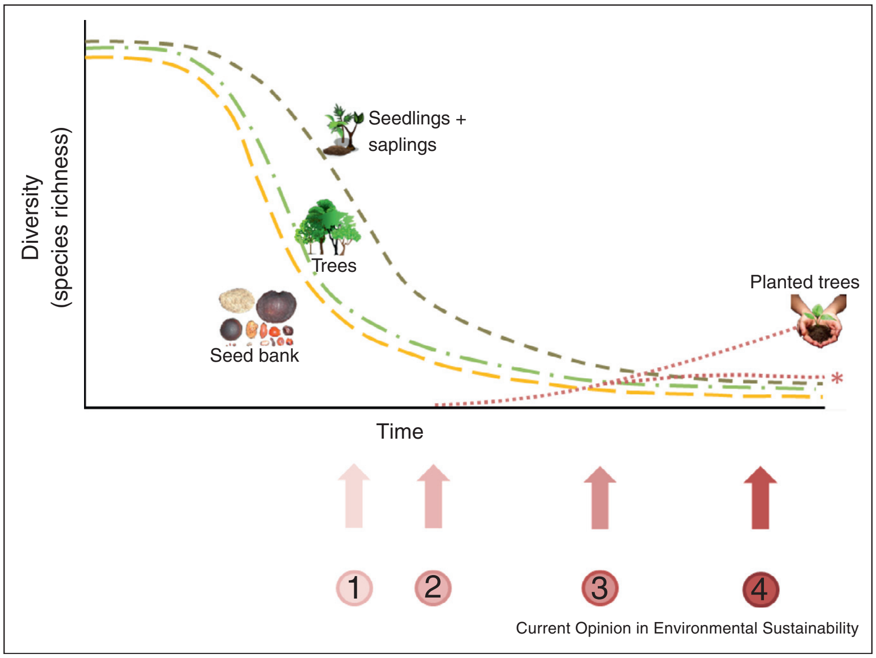
Trees under various types of agroforestry systems can originate from different sources (**A**, **B**, **C** in boxes). Trees from these sources are selected by ecological processes and farmers' criteria and contribute differently to alpha (plot-level) and beta (landscape-level) tree diversity. Varying proportions of trees from different origins, in different agroforestry systems, have different implications for tree diversity management.

reasons for people to use, tolerate, establish or remove trees [4] and the availability of and accessibility to planting materials (Figure 3). It is likely that the relative importance of such factors will change along the transition curve. For instance, at early stages of the forest transition, the type and density of new trees that spontaneously establish after disturbance events (natural or human-induced) depends on the density, diversity and viability of the seed bank in the soil (Figure 2). Replenishment of the seed bank depends on the presence of active processes generating new propagules from mother trees (e.g. pollination, seed production) and the activity of seed dispersal vectors. As land clearing expands, increased landscape fragmentation (larger distances between mature trees) and loss of habitat for dispersal vectors (fewer means to bring seeds to new places) affect the seed bank. Once a seed has germinated, the young plant has to survive, a fact that tree planting campaigns and restoration approaches often ignore [5]. Mortality rates of seedlings, saplings, poles and even adult trees might be high, because environmental conditions and management practices can create stressful environments. Together with competition with other plants, attacks from pests and diseases (biotic filters), and life history traits of the tree population, these stresses set limits to natural regeneration [6].

When natural dispersal and establishment processes are not sufficient for producing the full array of desired trees, there are two key points at which farmers can have a strong positive impact on the diversity of tree seedlings and saplings: (1) When farmers actively choose management practices that protect naturally regenerated trees (point 1; Figure 2); and (2) When farmers start transplanting wildlings (point 2; Figure 2). These practices will end up in 'forest domestication' [7–9]. Negative impacts on seedling diversity can be caused by management practices that aim to reduce competition for crops, by removal of species with little use, or by allowing domestic animals to forage during fallow periods. Where local regulations restrict farmers' access to trees on their land [10] or tree cover is used as a criterion to define protected areas, farmers may also choose to remove young trees to avoid future management and legal problems.

Farmers can also increase tree diversity and density using anthropogenic sources of indigenous or exotic planting material (planted or grafted), which are usually produced in on-farm or off-farm tree nurseries (point 3, Figure 2). At this point, the gene pool from which on-farm trees are derived depends on the characteristics of tree seed and seedling markets and supply systems, and/or social networks in which tree germplasm is passed on. Total

Figure 2



Schematic representation of the variation of tree diversity along the tree cover transition curve. Yellow and green curves represent expected patterns of diversity reduction of naturally occurring seedlings + saplings, trees and seed bank after forest clearing and agricultural intensification or urbanization with few tree components. Tree diversity curves are normalized based on a natural forest reference. Points 1–4 represent different entry points where active farmer selection and management decisions increase tree diversity: (1) through protection and management of natural regeneration, (2) through transplanting wildings, (3) through active planting from in or off-farm nurseries (seeds and grafted materials), and (4) through active tree selection and domestication. Curves in pink represent planted trees; see text for further explanation of the implications of tree planting for tree diversity.

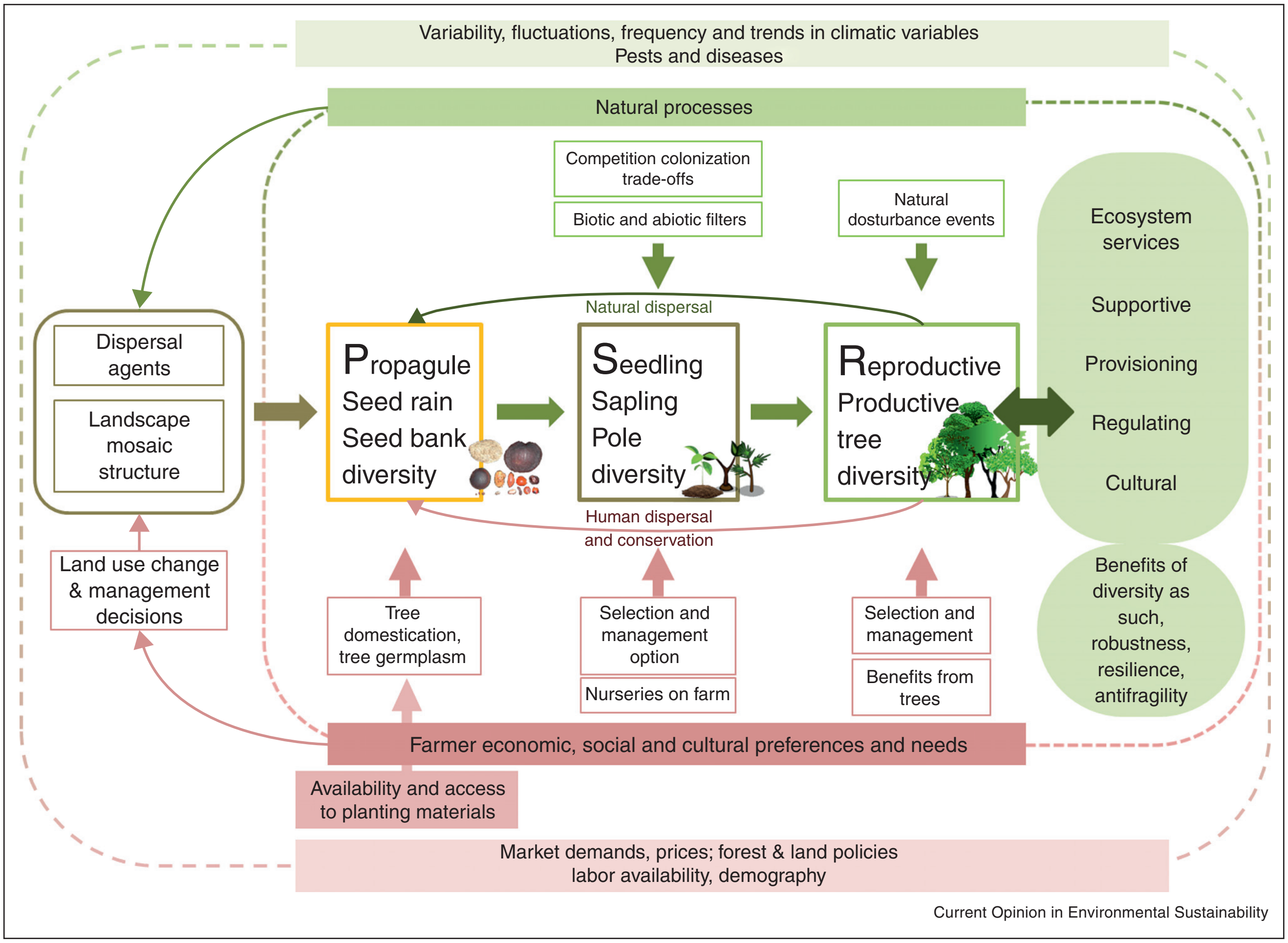
diversity might inadvertently be decimated (see (*) in Figure 2) when strongly centralized market players (such as government agencies, monopolistic or monopsonistic [11] traders) dominate the seed supply chain, or when species selection is based on ease of producing planting materials (e.g. most available) rather than local quality (local fitness) criteria. If this is the case, local knowledge associated with locally adapted tree material may easily disappear [12,13] and off-farm and circa-situm tree germplasm conservation becomes urgent [14••,15•,16]. Finally, where planted material and clones for grafting or cuttings (either stem or shoot cuttings) are subject to purposeful genetic selection, a process of 'tree domestication' may start [17,18,19•] (point 4, Figure 2). This process may lead to further reduction in tree diversity in landscapes, or maintain or promote landscape diversification, depending on the particular circumstances. Tree domestication may be part of an intensification process that leads to lower species diversity, or may support diversity when otherwise the less productive tree component of landscapes would be lost from it in competition with improvements in staple crop productivity [14••].

Management decisions by farmers also play a crucial role in defining adult tree density and diversity. Not all trees may be allowed to reach reproductive maturity, because they are frequently pruned, thinned or harvested for timber or other tree products [20,21].

Why tree diversity matters? — tree diversity impacts on ecosystem service provision and livelihoods

One of the main concerns about changes in tree cover and tree diversity is the impact of such changes on livelihoods and ecosystem services such as biodiversity conservation [22]. To understand the impacts of tree transitions on diversity dynamics, we need to understand the relationships between diversity, livelihoods and ecosystem services. There is an ongoing debate on whether biodiversity has to be conserved based on its intrinsic value, benefits of biodiversity as such (i.e. resilience, robustness or ''antifragility'' [23]; Figure 3) or mostly because of its relationship with ecosystem service provision. This debate is fueled by ethical considerations but also by lack of detailed understanding of the relationship between diversity and most ecosystem services (even though the necessity of a certain level of diversity is recognized) [24–26]. Quantifying this relationship requires multidisciplinary approaches and consideration of how different biodiversity dimensions

Figure 3

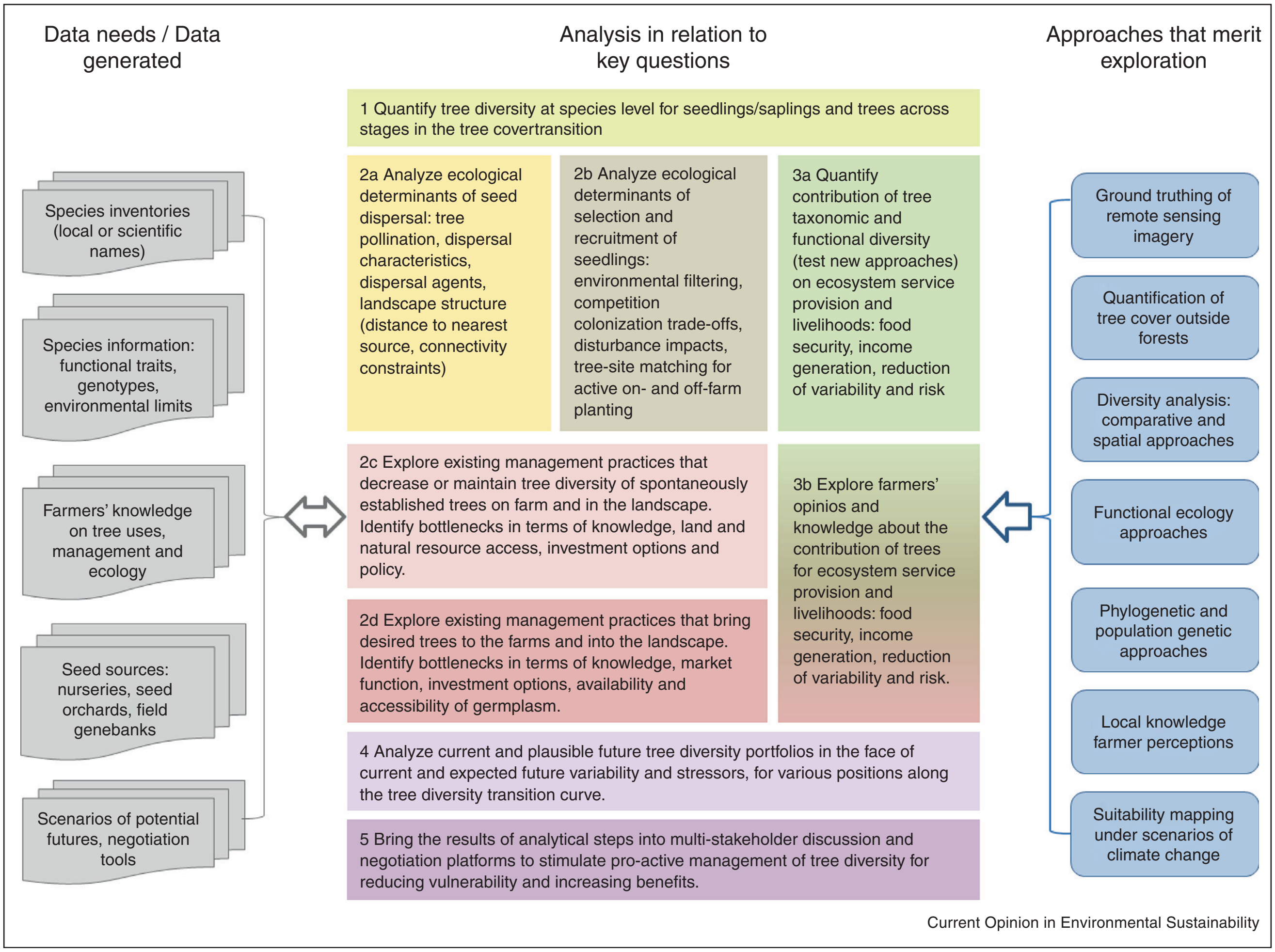


Analytical scheme for understanding the role of multiple factors affecting the dynamics of tree diversity – along the tree cover transition curve – and the benefits that humans derive from tree diversity on farm and in the landscape in the face of variability of abiotic, biotic and human factors.

(genetic distance, composition and function) are related to specific ecological processes that underpin ecosystem services [25]. For instance, recently there has been a shift of focus from looking purely at species richness, a common surrogate of diversity, to consideration of functional diversity [27] and its relation to ecosystem service provision [28]. This is of particular importance, because the balance between win–win situations or win–lose situations from the perspective of species richness, as a measure of diversity, might change when considering functional diversity [14••]. In agroforestry systems, farmers are often well aware of functionality within a wide context that includes the use of different products, differences in tree characteristics (for example, differences in fruiting phenology) or risk management options. They manage different species for different purposes, related to how trees affect crops, ecosystem processes and more importantly how trees contribute to their livelihoods [29]. Still, information on tree functionality is scattered and unbalanced. For instance, among more than 30,000 tree species from different regions of the world, included in different databases [30••], 47% do not have trait information; 32% have a coverage for 1–5 functional traits per species; and only about 3% of the species — the majority from temperate forests — have very detailed functional characterization (between 50 and 290 traits per species, using as the source for trait information the global plant trait database TRY, http://www.try-db.org/TryWeb/Home.php).

Functional diversity is most directly measured as the kind, average, range, and relative abundance of ‘‘functional traits’’ present in a given community. Use of this concept requires information on the composition of plant communities and knowledge on the traits that are relevant for particular ecosystem processes. Research on identification of key traits [31•] and development of standardized methods to measure them has evolved fast

Figure 4



Proposed steps for improving our understanding of processes that drive tree diversity patterns (at different stages of tree development) and impacts on ecosystem services and livelihoods.

in the last 10 years [32••], but most of the knowledge generated in functional trait research has come from natural communities. Recently conceptual frameworks have been proposed to test such approaches in human-ecological systems [33••], but active evaluation of these approaches and development of databases with required information (taxonomic composition, functional traits and farmer-perceived functions) are still lacking.

Understanding tree diversity dynamics in social-ecological systems

The framework presented above is a conceptual model that helps us understand the factors underlying the evolution [7–9,34] of certain patterns during the transition of natural ecosystems into agroforestry and other agro-ecosystems, as well as the potential implications for livelihoods and ecosystem services. The conceptual framework is also useful to identify potential gaps in knowledge, data, and analysis methods. The steps we propose highlight the databases needed for developing key areas of research (steps 1–5, Figure 4), as well as new approaches to improve our understanding of processes that drive tree diversity patterns along the tree transition curve.

The first step is to develop databases (Figure 4) that link species' identities (scientific and local names) with information on species. Species information could include functional traits, environmental limits (possibly obtained from species distribution models calibrated from geographical information on the point location distribution of species in relation to maps of bioclimatic variables; see [35] this issue), required facilitation by symbiotic soil organisms for survival and establishment [36] and farmers' knowledge on tree uses and ecology [37]. Such databases can be developed from existing data sources

[30••] for a relatively large number of species, and by active measurements of key attributes for sets of species where information is still sparse. For example, for the vast majority of agroforestry species there is no documented information on rooting characteristics, which is a key to modeling tree–crop interactions in agroforestry systems.

Data collection should focus on gathering information first about tree diversity of seedlings, saplings, and adult trees at different stages of the tree cover transition. This information in conjunction with ground truthing of remote sensing imagery (e.g. approaches for quantification of tree cover outside forests [38•]) and appropriate statistical methods for analyzing tree diversity [39,40] will be the keystone upon which research is built. For instance, linking information on tree abundance and diversity with tree attributes opens up research opportunities on the characterization of ecological determinants of seed dispersal [41], on seedling recruitment in different land use categories [42] and on the contribution of diversity to ecosystem service provision (3a).

Collection of information on management practices, farmers' opinions and local knowledge [37] is of key importance for identifying social, economic, or knowledge opportunities [34] and bottlenecks [14••] for the development of practices that maintain or increase tree diversity in farms and landscapes.

All new insights in ecological and social-economic processes could then be used to analyze current situations and scenarios of future tree diversity portfolios for various positions along the tree diversity transition curve [43•]. The final stage of this analytical approach, and the most important contribution, is to bring the results of these analyzes to discussion groups and negotiation platforms to stimulate pro-active management of tree diversity for reducing vulnerability and increasing benefits.

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Key terminology

Tree diversity: biological diversity (at gene, species and ecosystem level) as related to the woody perennial growth form found across many plant taxa. At species level, species richness and evenness in the abundance of component species and diversity of functional groups are commonly used indicators.

Plant functional traits: morphological, physiological and phenological characteristics which impact plant fitness via their effects on growth, reproduction and survival, the three components of individual performance.

Monopsony: is a market form in which only one buyer faces many sellers.

Antifragility: defined as the third pole in a triangle with robustness (neutral) and fragility (negative), based on a positive response to variability and disturbance.

Monopoly: market form when a specific person or enterprise is the only supplier of a particular commodity.