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Ecological integrity of tropical secondary forests: concepts and indicators

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ABSTRACT

Naturally regenerating forests or secondary forests (SFs) are a promising strategy for restoring large expanses of tropical forests at low cost and with high environmental benefits. This expectation is supported by the high resilience of tropical forests after natural disturbances, yet this resilience can be severely reduced by human impacts. Assessing the characteristics of SFs and their ecological integrity (EI) is essential to evaluating their role for conservation, restoration, and provisioning of ecosystem services. In this study, we aim to propose a concept and indicators that allow the assessment and classification of the EI of SFs. To this end, we review the literature to assess how EI has been addressed in different ecosystems and which indicators of EI are most commonly used for tropical forests. Building upon this knowledge we propose a modification of the concept of EI to embrace SFs and suggest indicators of EI that can be applied to different successional stages or stand ages. Additionally, we relate these indicators to ecosystem service provision in order to support the practical application of the theory. EI is generally defined as the ability of ecosystems to support and maintain composition, structure and function similar to the reference conditions of an undisturbed ecosystem. This definition does not consider the temporal dynamics of recovering ecosystems, such as SFs. Therefore, we suggest incorporation of an optimal successional trajectory as a reference in addition to the old-growth forest reference. The optimal successional trajectory represents the maximum EI that can be attained at each successional stage in a given region and enables the evaluation of EI at any given age class. We further suggest a list of indicators, the main ones being: compositional indicators (species diversity/richness and indicator species); structural indicators (basal area, heterogeneity of basal area and canopy cover); function indicators (tree growth and mortality); and landscape proxies (landscape heterogeneity, landscape

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connectivity). Finally, we discuss how this approach can assist in defining the value of SF patches to provide ecosystem services, restore forests and contribute to ecosystem conservation.

Key words: natural regeneration, secondary succession, ecological restoration, tropical forests, indicators, monitoring, vegetation structure, resilience.

CONTENTS

I. INTRODUCTION

The Anthropocene is an era of unprecedented human impacts on the environment, where large extents of natural ecosystems have been converted and transformed (Hansen *et al*., 2013). The level of ecosystem transformation has historically been associated with their ecological integrity (EI; for definitions of key terms see Table 1) (Karr & Dudley, 1981; Karr, Larson & Chu, 2022), with undisturbed ecosystems having higher EI – and therefore higher conservation value – and recovering systems having lower EI. This view ignores the temporal dynamics of ecosystem recovery and the fact that a recovering ecosystem can be functioning perfectly well despite being (still) very different from the undisturbed ones. While the concept of EI has helped set priorities for the conservation of ecosystems, it fails to protect recovering systems that might importantly contribute to ecosystem functioning and biodiversity conservation at different scales. Adapting the concept to allow assessment of the EI of systems during the recovery process is of utmost importance for land-use planning and efficient implementation of biodiversity conservation and ecosystem restoration in the Anthropocene.

Tropical forest regrowth covers approximately 600 million hectares (Pan *et al*., 2011) and plays a crucial role in biodiversity conservation and ecosystem service provision in human-modified landscapes (Chazdon, 2014; Matos *et al*., 2020). Under optimal conditions, successional or secondary forests (SFs) that regrow naturally after the abandonment of pasture and agricultural lands can attain many similar characteristics to mature forests within a few decades to centuries (Poorter *et al*., 2021). These SFs can harbour a high diversity of plants and animals (Chazdon *et al*., 2009), including many species useful to people (Toledo & Salick, 2006; Junqueira, Shepard Jr. & Clement, 2010), connect forest fragments (Arroyo-Rodríguez *et al*., 2017), sequester large amounts of carbon (Pan *et al*., 2007; Poorter *et al*., 2016) and conserve floristic distinctiveness of biomes (Jakovac *et al*., 2022). Under limiting conditions, however, succession can be arrested, and fail to restore ecosystem functions fully (Arroyo-Rodríguez *et al*., 2017). Differentiating these different ecological conditions along the stages of succession, i.e. before its full recovery, is essential for identifying the conservation and restoration value of SF patches and the need for management to accelerate recovery.

Decades of studies on tropical forest succession have identified how natural and anthropogenic drivers affect the capacity of forests to regenerate. Drivers operating at different spatial scales importantly affect the capacity of forests to regenerate and to return to levels similar to their original state, through their influence on species availability and performance (Pickett, Collins & Armesto, 1987). At the regional scale, climate and soil properties define productivity levels and functional characteristics that shape the divergent rates of recovery of different forest types (Poorter *et al*., 2016; Rozendaal *et al*., 2019). At the landscape scale, forest cover and configuration determine forest connectivity and consequently the availability of seeds and biotic dispersal agents (Robiglio & Sinclair, 2011; Arroyo-Rodríguez *et al*., 2017). At the local scale, previous and current land use determine local soil quality and *in situ* propagule availability such as seeds, stumps, or sprouts (Mesquita *et al*., 2001; Gehring, Denich & Vlek, 2005; Jakovac *et al*., 2021). SFs that regrow in fragmented landscapes and on sites with an intensive land-use history have a limited capacity to restore ecosystem functioning, reduced recovery rates of vegetation structure

Table 1. Terminology and definitions used in this study.

Term	Definition
Component (of EI)	Main group of elements that define the integrity of an ecosystem (composition, structure and function).
Ecological integrity (EI)	The capacity of a system to support and maintain a balanced, integrated, adaptive community of organisms with a species composition, diversity, and functional organization comparable to that of natural habitat of the region.
Ecological resilience	Ability of ecosystems to absorb changes of state variables and reorganize or adapt to multiple ecosystem equilibrium states.
Ecosystem attributes	Characteristics of an ecosystem that can be identified and potentially measured.
Ecosystem functioning	The outcome of a set of processes and ecological functions determined from biotic and abiotic interactions.
Ecosystem health	Specific types and rates of ecological processes and arrangement of structural elements that characterize diverse and productive ecosystems.
Ecosystem services	The benefits that people obtain from ecosystems (Millennium Ecosystem Assessment, 2005) or the contributions of ecosystem structure and function (in combination with other inputs) to human well-being (Burkhard & Maes, 2017).
Indicator	Ecosystem attribute or measure of environmentally relevant phenomena used to depict or evaluate ecosystem conditions and their changes or to set environmental goals (Heink & Kowarik, 2010; Prach *et al.*, 2019). A good indicator is easy to measure, is sensitive to stresses and has a known response to natural and anthropogenic disturbances and changes over time (Dale & Beyeler, 2001).
Mature reference state	Historical natural characteristics from an undisturbed ecosystem or an ecosystem in an advanced stage of succession.
Old-growth forest	A forest ecosystem that has grown for a long period of time (usually over 100 years old) and that harbours historically known characteristics associated with biodiversity and ecosystem functioning.
Resilience	See *Ecological resilience*.
Secondary forest (SF)	Regenerating forests growing after disturbances such as logging or complete land clearance of the original forest, usually on abandoned pastures or agricultural fields. SFs can originate from fully natural regeneration, assisted regeneration or active planting.
Succession (secondary succession)	Process of recovery of natural ecosystems following natural or anthropogenic disturbance events.

and diversity, and show altered species compositions (Styger *et al.*, 2007; Jakovac *et al.*, 2015; Mesquita *et al.*, 2015; Pinho *et al.*, 2018; César *et al.*, 2021; Heinrich *et al.*, 2021). Within a given forest type and region, therefore, the level of anthropogenic impact at the landscape and local levels ultimately determines the ecological condition of SFs and their capacity to recover ecosystem functioning fully.

We lack, however, a theoretical basis that allows classification of the ecological condition of SF patches during the recovery process, i.e. at different ages after abandonment. Current concepts of ecological condition, such as EI (Karr & Dudley, 1981; Karr *et al.*, 2022), use reference systems that can be decades away from early recovering forests, making reasonable comparisons difficult. Forest restoration assessments use average values from naturally regenerating forests as references for monitoring restoration success, ignoring that natural succession can be arrested. Setting intermediate benchmarks over time (Balaguer *et al.*, 2014) that reflect an optimal successional trajectory could facilitate the assessment of ecosystem recovery at different successional stages. Setting such benchmarks over the successional process requires recognizing the variation in successional pathways. Additionally, ecosystem attributes show different trajectories over time and different rates of recovery (Poorter *et al.*, 2021), potentially requiring different indicators for each successional level. The accumulated knowledge on the limiting conditions for succession and the drivers of multiple successional pathways can support the design of a concept and indicators that allow assessing and classifying the EI of different successional stages or stand age.

Herein we review the literature to understand how EI has been assessed in different ecosystems, and which EI indicators are commonly used for tropical forests. Specifically, we: (*i*) modify the concept of EI so that it embraces temporal dynamics and is applicable to SFs; (*ii*) identify a list of indicators that can be used to evaluate the EI of SFs; and (*iii*) associate indicators of EI to the provision of ecosystem services, in order to connect the theoretical concept with its societal relevance. This study synthesizes the literature to promote a theoretical basis for identifying and classifying the ecological condition of SFs, allowing for better land-use planning, and the implementation and monitoring of conservation and restoration initiatives. Eventually, this will help in achieving the ambitious climate-change mitigation goals (e.g. Bonn Challenge, Paris Agreement, and Trillion Trees programs; Brancalion & Holl, 2020) as well as efficiently implementing the targets for the UN Decade on Ecosystem Restoration.

II. MATERIALS AND METHODS

To identify the main concepts and indicators associated with EI, we conducted two separate literature searches in *Web of Science*. The first search aimed to identify and describe the concepts and main ecological components of EI, as applied to any ecosystem type (e.g. aquatic or terrestrial systems). The aim of this search was to obtain as broad an input as possible, to define a concept of EI that is relevant to (secondary) forests. The second search aimed to identify indicators that are specifically used to evaluate EI of forest systems.

The search string used for search #1 was: *TITLE = ('ecological integrity' OR 'ecological quality' OR 'ecological health' OR 'ecological resilience' OR 'biotic integrity' OR 'biotic quality' OR 'biotic health' OR 'biotic resilience' OR 'ecosystem integrity' OR 'ecosystem quality' OR 'ecosystem health' OR 'ecosystem resilience' OR 'forest integrity' OR 'forest quality' OR 'forest health' OR 'forest resilience')*. We thus searched using the most common concepts used to describe and assess some sort of ecological quality of ecosystems in order to identify a concept that was most likely to embrace SFs. We included combinations of the words *health*, *quality* and *resilience* as they may be used in the literature with a similar meaning to integrity. We restricted our search to review articles from environmental disciplines (Environmental science, Biodiversity conservation, Ecology, Forestry, Remote sensing, Geosciences multidisciplinary, Environmental studies, Physical Geography, Multidisciplinary sciences, Plant sciences, and Biology). This first search returned a total of 112 articles. We first screened the title and abstract from these articles, identifying if the main objective of the study revolved around concepts and/or indicators of EI in native ecosystems. This screening reduced the number of relevant articles to 50, which were then assessed by reading the main text to identify the concepts of EI used, and whether they represented a new concept or a citation of an older reference. We excluded nine articles that did not explicitly indicate the concept they were using, resulting in a total of 41 articles (Table S1). Additionally, we assessed the original studies cited within the compiled references if they were not located by our search and included these articles ($N = 6$; Table S1) and concepts in our final results. This search enabled us to identify not only the concepts associated with EI, but also the main components used to describe it.

For search #2, we focused on the indicators used to evaluate EI in forest ecosystems. This search was not constrained by methodology (search #1 was restricted to review articles), so it included original research studies using field data, modelling or remote-sensing approaches, as well as review articles. We used the same search string as above, with the additional terms: *AND TOPIC = (forest*) AND (indicator* OR metric*)*. This search was restricted to the same environmental disciplines listed above and returned a total of 140 articles. We performed an initial screening to remove studies focused on aquatic systems (e.g. mangrove, stream and wetland studies), non-forest native ecosystems (e.g. coastal vegetation, grassland or savanna, and urban forest), species or organism characteristics (i.e. not addressing EI directly, and studies that focused only on the effect of air pollutants and pathogens on tree health) and studies that did not clearly present a list of indicators. We also removed two studies that were not available for download. This resulted in a final total of 72 articles (Table S2). From each article, we extracted information on the study sites (region, history of disturbance), the indicators used to evaluate EI (indicator name and metric, and associated component of EI) and finally, the ecosystem services associated with each indicator (Table S3) as indicators of EI could be used to assess ecosystem services. For the most frequent indicators that resulted from our screening, we assessed, based on expert knowledge, the quality of its association with ecosystem services: categorized as good, fair or no direct association.

We assessed the suitability of these indicators to evaluate the EI of SFs based on the following main evaluation criteria: (*i*) its behaviour is known in different forest types and across successional trajectories; (*ii*) it is easy to measure, monitor and understand; and (*iii*) it can be used at different spatial scales (patch or landscape level). For our analysis we further subdivided these into five evaluation criteria, we: (*i*) used the most frequent indicators that resulted from our screening, which are those more commonly used and known to assess patterns and processes in ecological studies, and determined in which successional stage they most efficiently indicated variations in EI (early, intermediate or late); (*ii*) classified indicators according to sampling complexity (easy – rapid assessment; medium – requires some specific knowledge; or hard – complex indicator requiring specialized equipment); (*iii*) classified indicators according to sampling frequency required (single or multiple); (*iv*) classified indicators by main methodological approach required (field based, remote sensing, other); and (*v*) classified indicators according to the spatial scale assessed [local plot (patch) or landscape level]. See Table S3 and Appendix S1 for the full list of information extracted from articles. Based on this classification scheme and on our expertise, we thus identified and classified the indicators both in terms of usefulness to assess overall EI of SFs and on cost-effectiveness and applicability for ecological assessments and monitoring. We focus on individual metrics instead of compound indices comprising multiple indicators because individual indicators (*i*) are easier to interpret and to implement by a wide range of technicians, (*ii*) allow for the identification of management practices required to improve the EI of successional forests (whereas a compound index would require de-composing to interpret which metric is most influential), and because (*iii*) the suitability of indicators might change with successional age.

III. LITERATURE REVIEW

(1) Concepts and main components of EI

Among the 47 articles assessed for search #1, three main concepts were presented: ecological or biotic integrity, ecological resilience, and ecosystem or forest health. EI was first defined by Karr & Dudley (1981, p. 56), as '*[…] the capacity of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region. […] A system possessing integrity can withstand, and recover from most perturbations* *imposed by natural environmental processes, as well as many major disruptions induced by man*'. This concept was initially proposed to monitor aquatic systems, mainly with regard to water quality goals for human use (Karr & Dudley, 1981). It was later adapted by Parrish, Braun & Unnasch (2003, p. 852), as '*the ability of an ecological system to support and maintain a community of organisms that has species composition, diversity, and functional organization comparable to those of natural habitats within a region. An ecological system or species has integrity or is viable when its dominant ecological characteristics (e.g., elements of composition, structure, function, and ecological processes) occur within their natural ranges of variation and can withstand and recover from most perturbations imposed by natural environmental dynamics or human disruptions*'. Andreasen *et al.* (2001), who developed a terrestrial index of EI, and Tierney *et al.* (2009), who addressed the monitoring and evaluation of EI of forest ecosystems, are often incorrectly cited as the source of the concept, with the concepts they use being the ones proposed by Karr & Dudley (1981) and Parrish *et al.* (2003) as described above. For a detailed history of the concept of EI, its terms and usage, see Wurtzebach & Schultz (2016) and Roche & Campagne (2017).

Ecological resilience is implicitly included in the concepts discussed above, but it has often been used separately in the ecological literature. Holling (1973, p. 17) first defined ecological resilience as '*resilience determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist*'. Holling (1973) characterized stability as persistence of a system near or close to an equilibrium state and resilience as the amount of disturbance that a system can absorb without changing its state. More recently, Gunderson (2000) presented a review of ecological resilience theory and application, and proposed that no single mechanism can guarantee the maintenance of resilience. When a system experiences shifts into an undesirable state, a diversity of ecological processes allows the system to reorganize itself and return to a desirable state or to reorganize and adapt to the alternative condition.

Ecosystem health and forest health concepts correspond to different notions of the status of ecosystems. The use of the word 'health' comes from a human-centred utilitarian/instrumental perspective and was initially associated with organism-level measurements, e.g. tree health (Kolb, Wagner & Covington, 1994; Ferretti, 1997). The term 'health' can be used as a bridge between scientists and non-scientists regarding the values of ecosystems (Kolb *et al.*, 1994). Rapport (1989) and Costanza (1992) initially suggested approaches to characterize and measure the health of nature. In an ecosystem perspective, Kolb *et al.* (1994, p. 12) found great difficulty in applying the concept of health to such complex systems as forests, and suggested that a definition should include '*specific types and rates of ecological processes, and numbers and arrangement of structural elements that characterize diverse, productive, forest ecosystems in major biogeographic regions*'. Kolb *et al.* (1994, p. 12) also listed four essential elements in their definition of forest ecosystem health: '*(1) physical and biotic resources to support forest cover; (2) resistance to catastrophic change and/or ability to recover after catastrophe; (3) functional equilibrium between supply and demand of essential resources; and (4) diversity of seral stages and stand structures*'.

Regardless of the wording, all concepts presented above have similarities regarding the most important components that characterize EI, which include native species, structural and physical characteristics, ecosystem functioning and ability to recover after disturbance. Following the main components of EI proposed by Karr & Dudley (1981) and Parrish *et al.* (2003), which divided EI into composition, structure, and function, and the concepts of health discussed above, we further subdivide these three components into separate categories applicable to forest ecosystems (Table 2): (*i*) Composition has a single category – Biological diversity; (*ii*) Structure is subdivided into two categories – Vegetation structure, and Landscape structure and composition; and (*iii*) Function has three categories – Physical or environmental condition, Ecosystem functioning, and Resilience (see Table 1 for definitions). This enabled us to accommodate these concepts more explicitly and to classify indicators accordingly, encompassing different aspects of the integrity of natural ecosystems. These different categories encompass different spatial scales, from landscape-level attributes setting the landscape matrix context (landscape structure and composition) to patch conditions (biological diversity and vegetation structure), which together determine ecosystem functioning and resilience.

(2) Indicators and patterns across forest succession

Indicators are measurable characteristics of the ecosystem that are related to the ecosystem condition or state (Table 1). Indicators provide information on the current condition of an ecosystem and enable the evaluation of ecosystem development over time (Wurtzebach & Schultz, 2016). They can be used to assess levels of degradation of ecosystems and to identify the need for management interventions in order to achieve a specified goal. In the case of EI, indicators are related to composition, structure and function components. Good indicators should be concise and reflect changes in community and/or ecosystem attributes (Table 1), being able to be used by researchers and practitioners to monitor ecosystem recovery.

Based on our literature search, we found 58 indicators (Table 2; Appendix S2) and 33 indices (i.e. combinations of multiple indicators) used to evaluate forest EI (Table S4). For each group of indicators, we listed a number of indicator metrics (see Table S5 for full list) that were used in each study, either using field-based or remote-sensing approaches. Indices based on combinations of multiple metrics were used to evaluate broad ecosystem integrity (e.g. Ecological Resilience Index, Ecosystem Health Index, Index of Biotic Integrity; Table S4). From the full list of indicators, the 10 most frequently assessed indicators (Table 3) were related to composition (indicator species or group; species diversity or richness); structure (canopy cover and structure; herbaceous or shrub cover or abundance; landscape composition and

Table 2. Main components of ecological integrity (EI) (see Section III.1) and associated indicators (see Section III.2).

Main and (sub)components of EI	Associated indicators
Composition	
Biological diversity	Indicator species or group, phylogenetic traits, sapling and/or seedling composition, sapling and/or seedling diversity or richness, species composition, species composition dynamics, species distribution dynamics, species diversity or richness, species functional diversity, species functional traits or groups
Structure	
Vegetation structure	Canopy cover and structure, community structure (plant), habitat condition, herbaceous or shrub cover or abundance, sapling and/or seedling abundance, sapling and/or seedling condition and size, snag and coarse woody debris, stand age, surface reflectance indices, surface texture measures, tree abundance, tree crown attributes, tree size and biomass, vegetation cover
Landscape structure and composition	Anthropogenic pressure, habitat specialization, land-cover and land-use dynamics, landscape composition and heterogeneity, landscape connectivity and fragmentation, landscape diversity, patch abundance, patch size, topography
Function	
Physical or environmental condition	Chemical parameters of deposition, soil erosion, soil physical and/or chemical parameters, water regimes
Ecosystem functioning	Community health (animal), community structure dynamics, ecosystem service provision or monetary value, flower, fruit and seed attributes, growth and mortality, insect outbreak frequency or intensity, litter structure, productivity and carbon sequestration, recruitment, species functional traits or groups change, tree growth and mortality, trophic interactions, vegetation condition and damage, water-related processes (transpiration, water-use efficiency, etc.)
Resilience	Disturbance frequency or intensity, disturbance model, forest recovery rate, network resistance, productivity and carbon sequestration dynamics, resilience coefficient or score, trajectories of vegetation condition and damage

heterogeneity; landscape connectivity and fragmentation; tree size and biomass); and function (tree growth and mortality; vegetation condition and damage; soil physical and/or chemical parameters). Additionally, we indicate the quality of these indicators in terms of assessment of ecosystem services potentially provided by forests (Table 3).

IV. APPLICATION OF CONCEPTS AND INDICATORS TO SFS

(1) Including successional forests in the concept of EI

The EI concepts (described above) use a desirable state as a reference (Andreasen *et al.*, 2001; Wurtzebach & Schultz, 2016), which is usually a non-disturbed state, such as an old-growth forest located within the same region. This desirable state is often described through the natural range of values of multiple indicators. This assumes that the reference ecosystem holds the highest EI and the more similar a system is to its undisturbed original condition, the higher is its EI. This definition fails to incorporate changes in state condition during the process of forest regeneration, and consequently assumes that EI is directly dependent on the time since recovery started, i.e. the age of the SF. To acknowledge the successional dynamics, intermediate reference states should be considered, in addition to the undisturbed state, to represent the optimal successional trajectory. Our approach is very similar to that used in monitoring children's health: although there is a need to know the physical and mental conditions they must achieve by adulthood, it is more important to assess health across a trajectory of development and growth.

We modified the definition from Parrish *et al.* (2003) to allow it to be applied to and operationalized for SFs. Thus, we describe EI as 'the ability of an ecological system to support and maintain a community of organisms that has species composition, diversity, and functional organization comparable to those of natural habitats within a region *and at a given age class*. An ecological system has integrity when its dominant ecological characteristics/indicators (e.g. elements of composition, structure, and function) occur within an optimal natural range *for that specific age class (i.e. time since succession started)* and can withstand and recover from most perturbations imposed by natural environmental dynamics or human disruptions'. This means that SFs following successional trajectories under optimal conditions can serve as a reference for the maximum EI possibly attained at each successional stage (or age class) in a given region and forest type. Optimal conditions imply minimum limitations for successional processes, i.e. high species availability and favourable conditions for species performance. Such optimal conditions for forest succession can be found in forest gaps and in transformed landscapes with a land-use history of low intensity, duration and frequency and with a high forest cover (Fig. 1).

To make this concept operational, we propose that reference values of indicators are retrieved from two reference systems: an undisturbed or mature reference state (as historically used for EI) and an optimal successional

Table 3. The 10 most frequently assessed indicators of forest ecological integrity used in the literature and their associations with eight different ecosystem services. The number of papers that assessed each indicator is shown in parentheses. Bullet points indicate whether the indicator is categorized as good (●) or fair (○) in assessing ecosystem services; cells without bullet points indicate no direct association.

Indicator name	Climate regulation	Soil conservation	Pollination or pest control	Air quality or water regulation	Biodiversity conservation	Habitat integrity	Provision: wild fruits and seeds	Cultural services
Composition								
Species diversity or richness (24)					●			
Indicator species or group (21)			○		●	○	○	○
Structure								
Tree size and biomass (22)	●			○		●	○	○
Landscape connectivity and fragmentation (16)			○		○	○		
Canopy cover and structure (13)	●			○		○		
Herbaceous or shrub cover or abundance (13)	○	○			○	○		
Landscape composition and heterogeneity (11)	○	○		○		●		
Function								
Tree growth and mortality (14)	●							
Vegetation condition and damage (13)	○							
Soil physical and/or chemical parameters (11)		●						

trajectory. For the mature reference, a range of values must be identified that embrace the spatio-temporal variation in the absolute values of indicators found in old-growth forests or, in their absence, in forests in advanced stages of succession located in the same biogeographic region. For the optimal successional trajectory, values of indicators should be retrieved for different age classes or successional stages along trajectories under minimum limitations to succession. While limitations to succession reduce the EI of SFs, restoration and management practices have the potential to foster succession and improve the EI of SF patches (Fig. 1). The optimal successional trajectory can be expressed as absolute values (e.g. biomass values of 100 Mg ha^{-1} at 20 years) or as proportions relative to the old-growth forests in the region (e.g. early successional forests will show 10–20% of the value found in mature forests located in the region). Deviations from the natural range of values found in the optimal successional trajectory should be interpreted as a reduction or increase in EI (Fig. 1).

Building upon previously published EI concepts, we modify the concept of EI to add the temporal dynamics of SFs, allowing the assessment of EI across different successional stages. Previous studies have used mature forests and average values of naturally regenerating forests as references for monitoring forest restoration (e.g. Londe *et al.*, 2020), overlooking the large variation in successional pathways as a result of limitations to succession. Here we explicitly recognize the large variation in indicator values across successional trajectories and propose that an optimal successional trajectory should be used as a reference.

Operationalizing this reference of an optimal successional trajectory, however, can be challenging. Such reference systems may not exist in degraded landscapes or in entire regions that have an ancient history of intense anthropogenic transformation. To circumvent this limitation, modelling approaches using data from multiple landscapes could build scenarios of low anthropogenic impact to model optimal successional trajectories. Moreover, future studies should

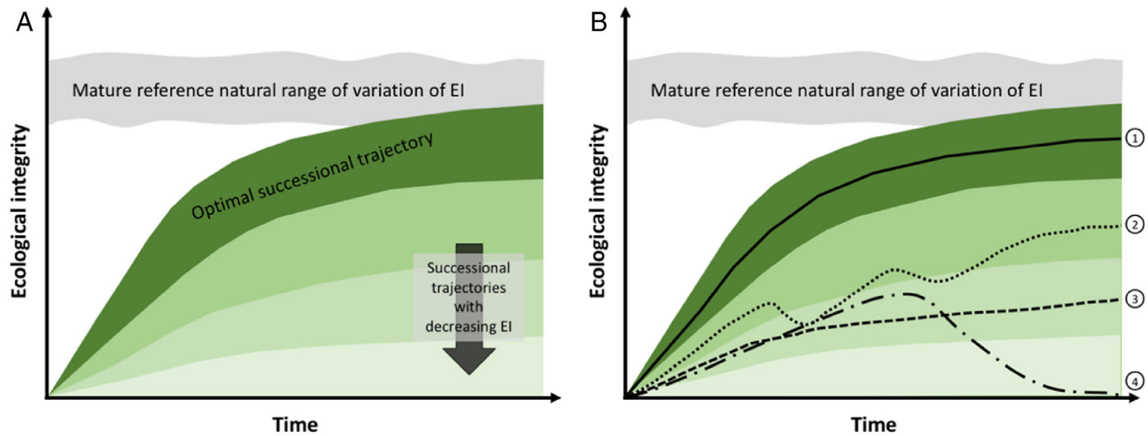

Fig. 1. (A) Diagram illustrating the concept of ecological integrity (EI) applied to secondary forests (SFs). It shows the change in EI over time and across different successional trajectories (green bands) arising from clear-cut forests and highlighting the optimal successional trajectory (dark green band). Green bands with lighter colours represent trajectories with decreasing EI. We can assess early, intermediate or late successional stages based on increasing levels of EI across time (A). In the upper portion of the graph (grey band), we show the natural range of variation of EI that exists in mature reference forests (e.g. old-growth forests) that represent the potential maximum EI that a site can achieve. In (B), we show different successional trajectories that may arise due to limitations to succession or disturbances: (1) optimal successional trajectory; (2) temporal variations decreasing the recovery rate; (3) rapid initial development, but stabilization in a suboptimal condition; and (4) positive initial recovery, but future degradation resulting from a strong disturbance (e.g. pest outbreak or extreme drought).

investigate whether optimum successional trajectories can be characterized by the proportional values of indicators in relation to the old-growth forest and whether these can be applied across regions. Additionally, studies should provide decision-makers with maps or tables of regionalized reference values for both old-growth forests and optimum successional trajectories using either data-based or model-based approaches.

(2) Successional trends of indicators

The successional behaviour of most of these frequently used indicators of EI (Table 3) is well known, especially for vegetation attributes (Finegan, 1996). A recent meta-analysis across a range of climatic conditions (*ca.* 1200–2500 mm of annual rainfall) showed that recovery to 90% of old-growth values is fastest for soils (<1 decade) and plant functions (<2.5 decades), intermediate for vegetation structure and species diversity (2.5–6 decades), and slowest for biomass and species composition (>12 decades) (Poorter *et al.*, 2021). Despite the large variation in successional pathways and rates of regrowth across landscapes (Norden *et al.*, 2015), predictable general patterns have been described and are summarized below for the most frequently used indicators of EI (Table 3). Tropical forest successional stages, following optimal trajectories (Fig. 1, dark green band), are summarized following Finegan (1996) as: early stage characterized by the colonization of herbs, shrubs and pioneer tree species (0–10 years of regrowth), intermediate stages when pioneer trees dominate the canopy (10–30 years) and late stages when pioneers are replaced by late-successional species (>30 years).

Within the composition component, as succession proceeds there is an increase in species diversity and richness and a replacement of indicator species and functional groups. Species richness recovers to 90% of old-growth forest values within 31 years on average while species composition can take more than 120 years or may never happen (Rozendaal *et al.*, 2019). Increment in species richness is very steep at early to intermediate successional stages and slows down at late stages (Rozendaal *et al.*, 2019). Overall successional changes in species composition are less predictable and can be extremely slow (Rozendaal *et al.*, 2019; Poorter *et al.*, 2021). Therefore, we recommend that changes in the presence and abundance of indicator species or specific groups of species are used in assessments of successional changes. The replacement of pioneer species by late-successional species happens at intermediate successional stages for adult trees (Finegan, 1996), as seedlings of late-successional species may be present from the early stages (Guariguata & Ostertag, 2001; Peña-Claros, 2003). SFs with lower EI will show slower species turnover and species richness, and higher dominance by certain indicator species and plant groups (Gehring *et al.*, 2005; Styger *et al.*, 2007; Jakovac *et al.*, 2016). These can be observed at all successional stages by showing lower species richness, higher abundances of non-tree life forms such as ferns, grasses, bamboos, vines, and lianas, and higher dominance by certain indicator tree species, compared to the reference trajectory (Gehring *et al.*, 2005; Styger *et al.*, 2007; Letcher & Chazdon, 2009; Jakovac *et al.*, 2016).

Within the structure component, during succession basal area and biomass accumulate and consequently canopy cover increases and herbaceous and shrub cover or abundance are reduced (Guariguata & Ostertag, 2001; Estrada-Villegas *et al.*, 2020). Total basal area tends to stabilize at intermediate successional stages while biomass and horizontal heterogeneity stabilizes at intermediate to late successional stages (Poorter *et al.*, 2021). As a consequence of plant colonization and the increase in basal area, canopy cover sharply increases and then stabilizes within early successional stages. SFs with lower EI will have lower average tree size and a more homogeneous tree-size distribution, showing lower basal area, biomass and canopy height and lower heterogeneity in tree size [e.g. Gini index of basal area or diameter at breast height (dbh)], compared to optimum reference trajectories (Marin-Spiotta, Ostertag & Silver, 2007; Chazdon *et al.*, 2010; Jakovac *et al.*, 2015; Mesquita *et al.*, 2015; Poorter *et al.*, 2016; Rozendaal *et al.*, 2019; Pérez-Cárdenas *et al.*, 2021). Landscape attributes, another commonly used indicator of structure, are not directly associated with successional changes, but can be used as proxies for the conditions enabling succession in the landscape (Arroyo-Rodríguez *et al.*, 2017; Jakovac *et al.*, 2021), and therefore can be used as indirect indicators of EI across successional stages.

Within the function component, during succession rates of tree growth decrease (Norden *et al.*, 2015) and mortality shows a hump-shaped relationship. Tree growth rates tend to be higher at early to intermediate stages of succession (Marin-Spiotta *et al.*, 2007) due to the rapid growth rates of pioneer and early secondary species (Chazdon *et al.*, 2010). Mortality rates tend to be higher at early to intermediate stages due to thinning and the mortality of same-aged pioneer species but are reduced at late stages (van Breugel, Martínez-Ramos & Bongers, 2006). Successional changes in soil conditions are less predictable, probably due to a dependence on geomorphological characteristics and the conditions left after land use (which can increase or decrease soil fertility, for example) (Powers & Marín-Spiotta, 2017). However, recent studies suggest that soil nitrogen, carbon stock and bulk density increase sharply and then stabilize within the early stages of succession (Poorter *et al.*, 2021; van der Sande *et al.*, 2023). SFs with lower EI will show slower dynamics and therefore lower rates of tree growth and mortality, and slower restoration of soil conditions, especially at early to intermediate stages of succession.

(3) Suggested indicators for assessing the EI of tropical SFs

Based on the list of indicators used most frequently in the literature (Table 3) and our evaluation criteria [known behaviour across successional trajectories, ease of measurement (sampling complexity and sampling frequency), methodological approach and spatial scale] we present in Table 4 a list of indicators for use in assessments of the EI of SFs. With this list, researchers and practitioners can identify the combination of indicators that best match their objectives and resources.

To evaluate the EI of SFs, at least one indicator for each component of EI (composition, structure and function) should be used. Across a range of characteristics, such indicators can be easy to measure, for example requiring single measurements from field surveys and allowing assessments at local scale, or they can be harder to obtain, requiring multiple measurements and remote-sensing techniques, but allowing assessments at regional scales (Table 4). Remote-sensing approaches require technologies that may not be available for local institutions, but are essential for upscaling the classification and monitoring of SFs, usually of interest for national governments and research institutions. Field-based evaluations tend to require less-specific technology and therefore are more accessible to a wide range of professionals and institutions. Some field-based indicators, such as species diversity, however, require expertise in species identification, potentially restricting their application, particularly in biodiversity hotspots. The list of indicators and evaluation criteria presented in Table 4 thus will enable the selection of indicators that are most suitable for different aims, spatial and temporal scales and resource availability.

Based on this literature review and on expert knowledge, we suggest a combination of the following indicators of composition and structure for assessing the EI of SFs at a local scale: indicator species or species richness, canopy cover, basal area and heterogeneity of basal area (or dbh). These indicators are easy to measure in the field and their recovery is associated with the recovery of function components, such as soil properties and plant functional traits (Poorter *et al.*, 2021). When using remote-sensing techniques, structure indicators can be assessed through metrics such as Leaf Area Index (LAI) and Normalized Difference Vegetation Index (NDVI), especially during early stages of succession (Table 4). For assessments of the EI of SFs at a regional scale, we suggest the inclusion of landscape structure indicators (e.g. landscape heterogeneity, landscape connectivity), which are known proxies for the capacity for recovery of composition, structure and function of SFs (Arroyo-Rodríguez *et al.*, 2017; Jakovac *et al.*, 2021).

It is important to highlight that reference values are required for two reference systems: a mature reference state and an optimal successional trajectory. The reference values of the optimal successional trajectory can be absolute values (and therefore region specific) or determined relative to the old-growth forest (and therefore comparable across regions). Future studies should try to identify relative values of indicators that can be used as an optimal successional trajectory in multiple regions. In addition, we suggest identifying indicator species and how patterns of species dominance change with EI and successional stages, as well as evaluating other indicators of function that are easier to assess in the field. Notably, some indicators will be more appropriate for generalization across regions (e.g. structure indicators) while others will be region specific (e.g. indicator species), therefore a combination of both may allow better characterization of EI given the heterogeneity of tropical plant communities.

V. ECOLOGICAL INTEGRITY, SOCIETAL DEMANDS AND IMPLICATIONS FOR DECISION MAKING

Ecological integrity is a concept applied to individual SF patches through the characterization of their composition,

Table 4. Suggested indicators for use in assessments of the ecological integrity of tropical secondary forests and evaluation criteria used to classify each indicator: successional stage (🟢 early, 🟡 intermediate, 🔴 late); sampling complexity (🟢 easy, 🟡 medium, 🔴 hard); sampling frequency required (🟢 single, 🔴 multiple); methodological approach (🟢 field based, 🔴 remote sensing); and spatial scale (🟢 local, 🔴 regional).

Indicator name	Indicator metrics suggested	Stage	Complexity	Frequency	Approach	Scale
Composition						
Species diversity or richness	Species diversity or richness	🟢🟡🔴	🟢🟡	🟢	🟢	🟢
Indicator species or group	Indicator species presence/abundance (e.g. successional groups, exotic species)	🟢🟡🔴	🟢	🟢	🟢	🟢
Structure						
Tree size and biomass	Tree basal area (total)	🟢🟡	🟢	🟢	🟢	🟢
	Tree basal area variation (e.g. standard deviation or Gini index)	🟡🔴	🟢	🟢	🟢	🟢
	Leaf Area Index (LAI)	🟢🟡	🔴	🟢	🔴	🟢🔴
	Normalized Difference Vegetation Index (NDVI)	🟢🟡	🔴	🟢	🔴	🟢🔴
Canopy cover and structure	Canopy cover (% ground cover)	🟢	🟢	🟢	🟢🔴	🟢🔴
Herbaceous or shrub cover or abundance	Ground vegetation cover (e.g. grass or light-demanding herbs)	🟢🟡	🟢	🟢	🟢	🟢
Landscape composition and heterogeneity	Landscape composition (land-use and land-cover types)	🟢🟡🔴	🟡	🟢	🔴	🔴
Landscape connectivity and fragmentation	Landscape connectivity or fragmentation	🟢🟡🔴	🟡🔴	🟢	🔴	🔴
Function						
Tree growth and mortality	changes in tree abundance or basal area	🟢🟡	🟢	🔴	🟢	🟢
	Tree growth and mortality	🟢🟡🔴	🟢🟡🔴	🔴	🟢🔴	🟢🔴
Vegetation condition and damage	Tree condition or damage (e.g. defoliation, damage to branches)	🟢🟡🔴	🟡🔴	🔴	🟢🔴	🟢🔴
Soil physical and/or chemical parameters	Soil organic matter, soil nitrogen content, bulk density	🟢🟡	🟡	🟢	🟢	🟢

structure, and function, providing information on the conservation and restoration potential of individual SF patches. From a societal perspective, however, the relevance of a SF patch will depend on its socio-ecological context. Therefore, the decision-making process on the socio-ecological value (and fate) of SF patches depends on an evaluation that combines the actual EI of a SF patch, the potential of a SF patch to undergo succession (and increase its EI), its potential to contribute to the resilience of the landscape as a whole, and the societal demand for land use (e.g. agricultural production, demand for ecosystem services).

From a socio-ecological perspective (Vieira *et al.*, 2014; Balvanera *et al.*, 2021), the value of SF patches therefore will greatly depend on the conditions of the landscape in which they are found. For example, in a highly deforested and fragmented landscape, SF patches with high EI will have high value for conservation and restoration, also contributing to landscape connectivity. These SFs with high EI will harbour high levels of biodiversity, contribute to ecosystem functioning and provide several ecosystem services including goods for people (such as food and materials). In the same highly fragmented landscape, SF patches with low EI may not have a high value for conservation at the patch level, but might play an important role for landscape connectivity and soil protection given the impoverished conditions of the landscape. In this case, actively managing these low-EI patches (e.g. climber cutting, invasive species control, enrichment planting, exclusion of cattle grazing) could foster succession and consequently increase their EI and the provision of ecosystem goods and services, also contributing to increased resilience of the landscape. Enhancing natural regeneration through management practices soon after agricultural abandonment is an easier and cheaper way of increasing its EI compared to managing older SF patches (Rezende & Vieira, 2019; Vieira *et al.*, 2021). Such low-EI SF patches could be managed for enhancing production through agroforestry, e.g. soil fertility or timber and non-timber production, and thereby contribute to the societal needs and goals for that specific landscape (Michon *et al.*, 2007; Chazdon, 2008; Diemont *et al.*, 2011; Heinrich *et al.*, 2021).

Therefore, the classification of the EI of a SF patch is only one step in the decision tree for land-use planning and landscape restoration. It is important to consider the social, legal, economic and political factors that influence the governance of SFs (Vieira *et al.*, 2014). To facilitate such discussions, we highlight four properties that should be assessed in SF patches to support decision-making on land-use planning: (*i*) the current EI of the SF – the higher its EI, the higher will be its conservation value; (*ii*) current provision of ecosystem services and societal needs – a better match between ecosystem services provided and societal needs, the higher will be the value of preserving and/or managing that SF patch; (*iii*) the role of the SF patch in the functioning and resilience of the landscape; and (*iv*) the trade-offs and synergies with local and regional societal demands. The combination of these four aspects should be considered in decision making for land-use planning in order to determine whether to conserve, manage or convert SF patches.

VI. CONCLUSIONS

(1) This study reviews the concept of EI and proposes adaptation of the concept to incorporate the temporal dynamics of recovering ecosystems such as SFs. We propose that the assessment of the EI of SFs uses two reference systems: a mature reference forest and an optimal successional trajectory. The mature forest is used to retrieve relative reference values, and the optimum successional trajectory serves as a reference for the maximum EI attainable at each age class or successional stage in a given region. The use of an optimal successional trajectory as a reference enables the evaluation of EI at any age class and successional stage.

(2) We provide a list of indicators that can be used to assess the EI of SF patches at different successional stages and associate them with the provision of ecosystem services. By detailing a list of indicators for assessing EI, we provide strategies for field and remote-sensing assessments and monitoring of forest recovery and restoration.

(3) Finally, we highlight that the socio-ecological value of SF patches extends beyond EI alone and might include the ecosystem services provided in their individual landscape contexts and for local societal demands and needs. SFs are seen variously as degraded forests by conservationists, as promising areas for forest restoration by restoration practitioners and researchers, as fallows by shifting cultivation farmers, and as an opportunity for agricultural intensification by agribusiness. Assessing the EI of SFs will help to identify their conservation value, and combined with a socio-ecological assessment will assist informed decisions on the fate of tropical SFs.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of 41 references obtained from search #1 in *Web of Science*, using search terms associated with the concept of ecological integrity, and the additional six references sourced from citations within these references.

Table S2. List of 72 references obtained from search #2 in *Web of Science*, using search terms related to indicators used to evaluate ecological integrity.

Table S3. Information associated with indicators used to evaluate ecological integrity (EI) that was taken from the papers selected from search #2.

Table S4. Indices used to assess overall ecological integrity of forests.

Table S5. List of indicator metrics used in assessments of ecological integrity.

Appendix S1. Excel spreadsheet with the full database from search #2 (raw data).

Appendix S2. Excel spreadsheet with full list of indicators and evaluation criteria and their associations with ecosystem services.

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