Assessing the resilience of global seasonally dry tropical forests

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SUMMARY

Seasonally dry tropical forests (SDTFs), a varied and extensive ecosystem type in the tropics, are characteristically adapted to seasonal water stress in zones of low rainfall. Land-use change, resource extraction, alien invasives, changes to the atmosphere, and changing fire and climatic regimes may have serious implications for the continued persistence of SDTFs. This paper assesses the extent to which SDTFs may be resilient in the face of these threats, considering their dynamics, community-level characteristics, and functional traits of constituent species. There is evidence that some SDTF biodiversity- and structure-related properties are resistant to low- to moderate-intensity disturbances and have the potential to recover after severe, even chronic, disturbances, at timescales in the order of decades. Although global SDTFs are, on average, not necessarily more resilient than moist tropical forests (MTFs), they may be more resilient to particular disturbances such as fires and drought. SDTFs are vulnerable to regime shifts and there is considerable uncertainty about their future under a changing climate and its interactions with other anthropogenic effects.

Keywords: disturbance, succession, fire, anthropogenic effects, climate change

Evaluation de la résistance des forêts tropicales à sècheresse saisonnière

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Les forêts tropicales à sècheresse saisonnière (SDTFs), un type d'écosystème étendu et varié dans les tropiques, sont adaptées de manière caractéristique au stress dû au manque d'eau dans les zones de faible précipitations. Les changements d'utilisation des terres, l'extraction des ressources, les espèces étrangères envahissantes, Les changements atmosphériques et les régimes climatiques et des feux changeants pourraient avoir des implications sérieuses sur une continuation de la persistance des SDTFs. Ce papier évalue jusqu'où les SDTFs peuvent être résistantes face à ces menaces, en considérant leurs dynamiques, leurs caractéristiques au niveau communautaire, et les traits de fonctionnement des espèces les constituant. Des preuves émergent qu'une partie de la biodiversité et des propriétés liées à la structure des SDTFs est résistante aux dérangements faibles à modérés et que celles-ci détiennent un potentiel de rétablissement après des désordres sévères, et même chroniques, dans une échelle de temps, ordonnée par décennies. Bien que les SDTFs globales ne soient généralement pas nécessairement plus résistantes que les forêts tropicales humides (MTFs), elles pourraient faire preuve d'une plus grande résistance face à certains sinistres tels que le feu et la sècheresse. Les SDTFs sont vulnérables aux changements de régime, et une question considérable demeure quant à leur futur dans un climat changeant et ses interactions avec d'autres effets anthropogéniques.

Evaluación de la resiliencia global del bosque seco tropical

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El bosque seco tropical (BST) es un tipo de ecosistema variado y extenso de los trópicos que se adapta característicamente al estrés hídrico estacional en zonas de baja precipitación. Los cambios de uso del suelo, la extracción de recursos, las especies exóticas invasoras, los cambios en la atmósfera, y los cambios en los regímenes de incendios y del clima pueden tener graves consecuencias para la persistencia continuada del BST. Este artículo evalúa el grado de resiliencia que puede alcanzar el BST frente a estas amenazas, teniendo en cuenta su dinámica, sus características a nivel de comunidad, y los rasgos funcionales de las especies que lo constituyen. Existen pruebas de que algunas propiedades del BST relacionadas con la biodiversidad y su estructura muestran resistencia a perturbaciones de intensidad baja a moderada y tienen potencial para recuperarse después de trastornos graves, o incluso crónicos, en escalas temporales del orden de décadas. Aunque en promedio y a nivel global el BST no es necesariamente más resiliente que el bosque húmedo tropical, si pudiera serlo frente a ciertas perturbaciones como los incendios y la sequía. El BST es vulnerable a los cambios de régimen y existe bastante incertidumbre sobre su futuro en un clima cambiante y debido a sus interacciones con otros efectos antropogénicos.

INTRODUCTION

SDTFs are a globally-threatened ecosystem that largely remain outside protected areas (Janzen 1988, Miles *et al.* 2006). Compared to MTFs, they tend to occur in conditions that happen to be favorable for human use: fertile soils, relatively flat topographies, and a drier, seasonal climate that suppresses pathogens, agricultural pests and weeds, supports shorter-statured vegetation that is easier to clear – a process facilitated by anthropogenic or natural dry-season fires – and allows for cultivation of short-cycle crops (Tosi and Voertman 1964, Murphy and Lugo 1986, Janzen 1988, Maass 1995, Fajardo *et al.* 2005). Indeed, SDTFs are regarded as the first frontier of human land-use change (Sanchez-Azofeifa and Portillo-Quintero 2011) and deforestation rates of SDTFs are believed to be higher than those of MTFs (Aldhous 1993). It is perhaps for these reasons that a greater proportion of tropical and subtropical dry forests (48.5% globally) are estimated to have been converted to human-dominated uses compared with any other terrestrial biome (Hoekstra *et al.* 2005). Yet, compared to MTFs, SDTFs remain understudied and underrepresented in the scientific literature: for instance, in over a 60-year period spanning 1945-2004, only ~14% of indexed references on Neotropical forests came from SDTFs (Sánchez-Azofeifa *et al.* 2005).

SDTFs are impacted by a variety of natural and anthropogenic disturbances (Miles *et al.* 2006, Dale 2011, Sanchez-Azofeifa and Portillo-Quintero 2011). Local anthropogenic effects include local land-use conversion (agricultural fields, pastures, urban land uses), resource extraction (including livestock grazing, hunting, extraction of wood and various non-wood forest produce), introduction of alien invasive species, and modification of natural disturbance regimes including fire regimes. Global anthropogenic effects include changes to the atmosphere and climate driven by anthropogenic emissions and remote land-cover change (Wright 2005). Our limited understanding of SDTF responses to the continued existence of anthropogenic disturbances necessitates a global assessment of their stability and resilience.

Such an assessment is especially pertinent in the current context of global change. The global atmospheric concentration of CO_2 is already higher than it ever was in the last 650,000 years and will continue to rise. Inherent uncertainty in prediction notwithstanding, there is consensus that by the end of the 21st century global average surface temperatures will rise compared to current levels (1.1-6.4°C depending on emissions scenario), accompanied by more intense, longer lasting, and more frequent heat waves (IPCC 2007). The tropics have been witness to increasing uncertainty in the intensity, arrival, and duration of rainfall over the past century (Feng *et al.* 2013). Extremes of daily rainfall are likely to increase in many regions in the future, while global projections suggest a general increase in tropical rainfall maxima and decreases in the subtropics (IPCC 2007). Annual mean warming in all regions SDTFs are found in is likely to be greater than the global mean warming, except in Australia and Southeast Asia, where it is likely to equal the global mean (IPCC 2007). Regional rainfall predictions are idiosyncratic and currently less robust in the tropics, with annual rainfall likely to increase in some places (e.g. East Africa) and decrease in others (e.g. most of Central America). Changes in rainfall can impact various ecosystem processes: for instance, phosphorous cycling is particularly sensitive to variation in rainfall in phosphorous-limited Neotropical SDTFs (Jaramillo *et al.* 2011). Global change can thus potentially further alter SDTF distribution and composition, and may interact with existing drivers in unexpected ways (Dale *et al.* 2001, Wright 2005).

The importance of tropical forests as carbon sinks in the present and near future is widely acknowledged (IPCC 2007). The contribution of SDTFs to this global pool, while presently unknown, is probably substantial: for instance, a study in Mexico estimated total biomass and soil carbon reserves of 141 Mg ha^{-1} from SDTFs, compared to 414 Mg ha^{-1} from MTFs (Jaramillo *et al.* 2003). SDTFs are also important for the range of diversity they harbor. Several insect families including ant lions (Mymeleontidae) and certain beetles (Trogidae, Tenebrionidae, Meloidae, etc.) are known to be more speciose in SDTFs as compared to MTFs (Hanson 2011). In some SDTFs, bird and mammal species richness may exceed that of wet forests (Murphy and Lugo 1995). In the Neotropics, although SDTFs have lower vertebrate species richness as compared to MTFs, they host numerous endemic species (Ceballos 1995). Some insular SDTF floristic nuclei host up to ~77% unique, though not necessarily endemic, plant species (Linares-Palomino *et al.* 2011). SDTFs also have greater structural and physiological diversity of plant life-forms than MTFs (Medina 1995).

A useful assessment of SDTF resilience may be approached by studying the parts that make up the ecosystem: in this case, the organismal adaptations and interactions that are relevant to the persistence of individuals, species, and functional groups that comprise SDTFs. In this approach, biodiversity – genetic, organismal, and ecological diversity (Harper and Hawksworth 1994) – is treated as an emergent property. A complementary approach studies the ecosystem as a whole, building on the large body of research linking ecosystem functioning – the pools and fluxes of materials and energy, and the services rendered to humans – to biodiversity (Hooper *et al.* 2005). Of particular interest is the link between biodiversity and ecosystem stability and resilience (e.g. Peterson *et al.* 1998, Elmqvist *et al.* 2003). The latter approach also provides tools to assess ecosystem resilience based on highly-aggregated data that are easier to measure than the data required for the former, more mechanistic approach.

The paper is organized as follows. First, the definition of global SDTFs is briefly discussed. Next, a framework and associated terminology is introduced to help better describe and analyze SDTF dynamics. The resilience of SDTF to various disturbances is then examined. Finally, studies relevant to SDTF persistence under global change are reviewed and a concluding synthesis provided.

The review focuses on studies of SDTF plants, and woody plants in particular. Exclusion of studies of other biota (e.g. animals, fungi) within this ecosystem is acknowledged as an important limitation that will hopefully be addressed in future studies. However, studies of disturbance impacts on other SDTF biota are included to the extent that they have important cascading effects on woody plant responses. The focus on woody plants reflects, to an extent, the literature trend.

SDTF DEFINITION

An understanding of SDTF change is dependent on how SDTFs are defined. The definition we adopt is the one used by several authors to define SDTFs globally – based on Holdridge's (1967) bioclimatic-envelope classification scheme – as forests with mean annual temperature typically greater than 17°C, mean annual precipitation (MAP) ranging from 250-2000 mm, 4-6 dry months (precipitation < 100mm), and an annual ratio of potential evapotranspiration to precipitation of greater than 1 (Murphy and Lugo 1986, Dirzo *et al.* 2011). Such conditions occur in the tropics, with the strong seasonality in precipitation largely driven by the north-south migration of the inter-tropical convergence zone (ITCZ) as it tracks the sun's changing zenith position during the year (Balek 1983); for this reason, the dry season typically overlaps with the cold weather season. Note that this definition encompasses forests that may be referred to in the literature by other names, but are included in this review, such as the monsoon rainforests and dry rainforests of northern Australia (e.g. Russell-Smith 1991, Fensham 1995).

There are two problems with such a definition, both relevant to projecting future distributions of SDTF under drivers such as climate change and fire. Firstly, precipitation regimes in regional SDTFs definitions differ notably (Gerhardt and Hytteborn 1992 and references within this paragraph). Whereas SDTFs in Latin America occur in regions with MAP up to 1600mm and a dry season that lasts at least 5-6 months (Gentry 1995, Pennington and Ratter 2010), in Africa they occur in regions with as few as 3 (Menaut *et al.* 1995) and as many as 10 dry months (Swaine 1992). In Thailand, areas receiving more than 2000mm of rain annually and as few as 2-3 dry months are classified as SDTF based on ecological characteristics and biogeographic affinities (Rundel and Boonpragob 1995, Bunyavejchewin *et al.* 2011). Recognizing this difficulty, Mooney *et al.* (1995) suggest that "in the simplest terms, they are forests occurring in the tropical regions where there are several months of severe, even absolute, drought." Strong seasonality in water availability, then, is the key unifying characteristic of SDTFs globally. The recognition of the inhomogeneity encompassed by the umbrella term "SDTF" is particularly important when predicting how SDTF ranges will track future climatic envelopes. This highlights the necessity of regional-scale characterization of SDTF precipitation regimes. Other characteristics such as fire are considered to be integral to ecosystem dynamics in some SDTFs (the paleotropics and Australia; e.g. Banfai and Bowman 2006, Timberlake *et al.* 2010, McShea and Davies 2011) but not in others (the neotropics; e.g. Sanchez-Azofeifa and Portillo-Quintero 2011). Similarly, SDTFs are, in some regions, closed-canopied by definition, but include open-canopied forests in others.

A second problem with bioclimatic-envelope based definitions is that globally, savannas frequently co-occur with SDTFs within the same climatic conditions (Murphy and Lugo 1986, Swaine 1992, Mooney *et al.* 1995, Bowman *et al.* 1999). Although savannas are often differentiated from forests based on fire regimes, tree cover, tree deciduousness, and the existence of a grassy understorey, it may difficult to distinguish degraded forest from mesic savanna based on these metrics alone. Forest and savanna may be more reliably distinguished by plant traits (Ratnam *et al.* 2011). In fact, the two are believed to be alternative stable states that, within a climatic regime, are governed by fire frequency and factors that affect tree growth, such as soil nutrient status (Hoffmann *et al.* 2012, Murphy and Bowman 2012). Therefore, while savanna and SDTF are distinct, and savanna studies excluded from this review, studies of transitions between SDTF and savanna or other ecosystems are important to assessing SDTF resilience and are therefore included.

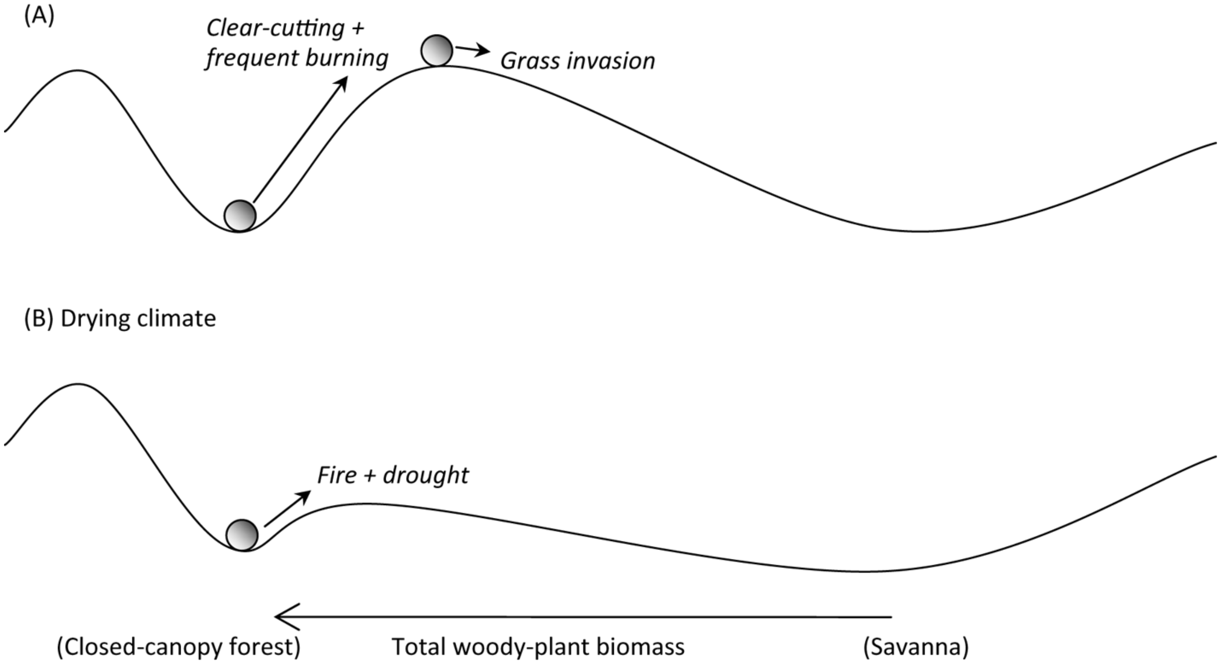
ECOSYSTEM STABILITY AND RESILIENCE CONCEPTS

Adaptive cycles and the stability landscape

The dynamics of SDTFs are usefully described in terms of "adaptive cycles" (Holling 2001, Walker *et al.* 2004); the reader is referred to those sources for a detailed treatment of concepts – mentioned briefly here – that frame this review. Walker *et al.* (2004) define ecological resilience as "the capacity of a[n] [eco]system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks." Concepts related to resilience can be visualized using a "stability landscape" (Figure 1). For brevity, we hereafter use the term "ecological resilience" as defined above, and the unqualified term "resilience" (or "ecosystem resilience") to mean one or more resilience components: resistance, stability, and ecological resilience.

The state of the ecosystem is changed by drivers or disturbances that could be endogenous or exogenous; while the ecosystem naturally tends to move towards the equilibrium position at the bottom of the valley it is in, disturbances tend to shift it out of equilibrium. Once close to a threshold, a relatively small disturbance can shift the ecosystem to an

FIGURE 1 *A stability landscape: balls represent states of an ecosystem (where a state is defined by a set of variables such as biomass or species richness), arrows represent drivers or disturbances and are labeled in* italics, *valleys represent regimes ("stability domains", "basins of attraction"), and peaks represent thresholds (also known as "tipping points"). Valley widths determine resilience. Valley slopes determine both how difficult it is to change the state of the ecosystem (a property termed "resistance", which is a component of resilience) and, once changed, how quickly it returns to its original state (a property termed "stability" or "engineering resilience"). This hypothetical example illustrates a one-dimensional landscape with a single state variable (total woody-plant biomass). Drivers can bring an ecosystem closer to a threshold by (A) changing its state, or by (B) reducing its resilience (equivalent to shrinking the valley the ecosystem is in) while its state – total woody-plant biomass – remains largely unchanged due to, for example, "demographic inertia." Once close to a threshold, a relatively small disturbance can result in a regime shift. See text for details. After Gunderson (2000).*



alternate regime during the reorganization phase (Scheffer *et al.* 2001, Walker *et al.* 2004). Modifications to the stability landscape can shift an ecosystem to an alternate regime without changing its state (Walker *et al.* 2004), in which case it may be "out of equilibrium" and tending towards the alternate attractor. For example, rapidly drying climate may move a forest ecosystem into a savanna regime, but forest dieback may be delayed due to "demographic inertia", caused by long lifespans and slow community turnover of trees, and "microclimatic inertia", caused by local modification of microclimate by the forest itself (Malhi *et al.* 2009, see also Sato and Ise 2012). Janzen (1988) suggested that SDTFs are particularly prone to demographic inertia wherein long-lived trees in disturbed SDTF die without replacement either due to lack of pollinators, seed dispersers, or adequate conditions for growth and development of juveniles. Such examples illustrate the potential difficulties in assessing ecosystem resilience or proximity to thresholds. One approach is to employ "early-warning indicators" of impending regime shifts that are independent of the specific ecosystem or disturbance mechanism but instead rely on sensing characteristic changes that occur to an ecosystem's state variables as it approaches a threshold (e.g. Guttal and Jayaprakash 2008; references therein). Biodiversity measures may also act as indicators of ecosystem resilience.

Ecological memory

For an ecosystem to continue to remain in the SDTF regime after disturbance, biological legacies from the original community (e.g. surviving plants, soil seed banks, or vegetative propagules) must be present during the reorganization phase. Recovery of the original structure and function is also reliant on the presence of seed dispersers, soil biota, pollinators, and other mutualists. The presence of such biological legacies, called "ecological memory" (Bengtsson et al. 2003), therefore determines the resilience of forests. Legacies within disturbed sites (e.g. stumps, root stocks, soil seed banks, soil biota) are called "internal ecological memory." An adaptive cycle at one scale also draws ecological memory from cycles operating at larger spatial and slower temporal scales (Holling 2001): for example, succession in an abandoned agricultural field is affected by propagules from external sources in intact or degraded forest patches in the surrounding landscape matrix ("external ecological memory"). The existence of such patches may also facilitate migration and is particularly relevant to forest resilience in the face of climatic change (McConkey *et al.* 2012).

ASSESSING SDTF RESILIENCE

Quantitatively, "SDTF resilience" in itself carries no meaning and must be further qualified, i.e., the resilience *of* particular ecosystem state variables (e.g. biomass stocks and fluxes, species richness, nitrogen-fixation rate) *to* particular disturbances (e.g. burning) or, when further precision is called for, disturbance regimes (e.g. annual early-dry-season burning). The relevant literature is vast and varied, and may be organized into:

- Studies of impacts of various disturbances on SDTFs. Where ecosystem state variables remain largely unchanged, these studies inform us on SDTF resistance, as defined previously. Where state variables have changed considerably, these studies inform us on SDTF stability or ecological resilience, as defined previously. In particular, studies of SDTF recovery or succession (based on both chronosequence, i.e. space-for-time substitution, and longitudinal studies) provide quantitative estimates of stability and are summarized in Table 1.
- Studies of community-level characteristics or species traits that are potentially relevant to SDTF resilience to various disturbances and are largely summarized in the trait-disturbance matrix in Table 2.

The review is largely evidence-based, emphasizing studies from SDTFs. Where these are lacking, evidence from meta-analyses and global reviews are included. Comparisons with MTFs are frequently made, reflecting literature trends.

A few caveats must first be mentioned. First, it is evident from Tables 1 and 2 that generalizations that apply to all SDTFs are difficult to develop – this is partly a result of the structural and compositional variation across SDTFs, sometimes even within the same biogeographic region (e.g. Menaut *et al.* 1995, Rundel and Boonpragob 1995). More region- or landscape-specific studies of SDTF resilience can help distinguish SDTF responses that are globally convergent from those that are not. Second, as is widely recognized (e.g. Klemens *et al.* 2011), SDTF resilience assessments must be viewed in light of the fact that very few old-growth SDTFs remain today that can be used as a baseline to compare against. Third, anthropogenic effects on SDTFs are superimposed on a background of natural dynamics, occurring at multiple spatial and temporal scales, which include transitions to and from other formations. For example, Menaut *et al.* (1995) suggest that SDTF, woodland, and savanna have long co-occurred in Africa with their distributions in space and time mediated by a variety of dynamic processes. These issues call for more paleoecological and long-term studies in relatively undisturbed forests that can serve as controls against which the effects of modified or novel disturbance regimes can be assessed.

Studies of impacts of disturbances on SDTFs

Disturbances such as land-use intensification, habitat fragmentation, invasive species, or fire in tropical and subtropical dry forests have generally been reported to result in species losses (e.g. Saha and Howe 2003, Sagar *et al.* 2003, Litton *et al.* 2006, Parthasarathy *et al.* 2008, Sapkota *et al.* 2009, Sundaram and Hiremath 2012, Cuneo and Leishman 2013) or reduced genetic diversity (Quesada *et al.* 2011). However, constant, or even increased, species richness, species density, or stem density after mild or moderate, largely anthropogenic disturbances have also been reported, attributed to removal of dominants, increased resource availability, guild-specific effects, or increased resprouting vigor (Sahu *et al.* 2008, Ramesh *et al.* 2009b, Sapkota *et al.* 2009, Ramaswami and Sukumar 2011, 2013, Baithalu *et al.* 2013). In a northern Australian SDTF, Fensham (1996) was unable to detect obvious direct detrimental effects of cattle grazing on the forest. In hurricane-prone SDTFs, species richness after hurricanes may remain essentially unchanged despite complete canopy defoliation and heavy mortality, although there may be compositional shifts (Van Bloem *et al.* 2005, Imbert and Portecop 2008). Fires in SDTF, which are generally of low to medium intensity and confined to the understorey (Stott 1986, Swaine 1992, Andersen *et al.* 2005, Kodandapani *et al.* 2008, Bunyavejchewin *et al.* 2011), result in relatively low large-tree mortality (Swaine 1992, Marod *et al.* 1999, Pinard *et al.* 1999, Sukumar *et al.* 2005, Suresh *et al.* 2010, Bunyavejchewin *et al.* 2011), despite high seed and seedling mortality (Kennard *et al.* 2002, Saha and Howe 2003, Vieira and Scariot 2006). This is especially true of early-dry-season fires compared to late-dry-season fires – numerous experiments have shown that woody forest species are less sensitive to the former than to the latter (Brookman-Amissah *et al.* 1980). The impact of such relatively low-intensity fires contrast with catastrophic high-intensity canopy fires in other ecosystems, such as dry forests in the temperate regions of Australia (Wotton *et al.* 2012, McCaw 2013). These observations suggest that some biodiversity- and structure-related properties of SDTFs may be resistant to low-intensity disturbances.

The studies listed in Table 1 illustrate that, after a variety of severe disturbances such as slash-and-burn agriculture, logging, conversion to pasture or urban land-uses, fires, hurricanes, or landslides, variables such as canopy cover and height, biomass, species diversity, stem density, mortality rate, or leaf area index, are estimated to recover to (or exceed) mature forest – or oldest successional site in study – levels in the order of a few to several decades. In general, basal area and biomass appear to be slowest variables to recover regardless of disturbance type (see also Lugo *et al.* 2002). The relatively quick recovery of leaf area index, canopy cover, and canopy height possibly reflect preferential allocation towards resource-acquiring structures early in woody-plant development (Brown and Lugo 1990, Lebrija-Trejos *et al.* 2008). Most SDTF succession studies do not measure belowground biomass (BGB), but its inclusion is predicted to reduce total ecosystem biomass recovery time estimates by about a decade, due to faster BGB accumulation rates (Vargas *et al.*

TABLE 1 *Temporal stability of SDTF biodiversity and structure after severe disturbances. Studies are sorted by increasing study site P (where P is a range, the mean P was used during sorting). Percent recovery compares successional vegetation to either vegetation in nearby mature forest or the oldest successional site included the study, with the latter indicated by a dagger (†); approximate recovery times inferred from text are indicated by a tilde (~); see corresponding reference for details on each study. A dry month was most commonly defined as a month with precipitation < 100mm; alternate or unspecified definitions are indicated by an asterisk (*); see corresponding reference for details.*

Site and climate (P, dry months, T)	**Treatment or disturbance**	**Variable**	**Age in years (% recovery)**	**Reference**
Mexico (746mm, 7 mo.*, 25°C)	Clear-cutting, bulldozer, fire, housing or pasture or abandonment	Mean tree density Mean basal area	24-27 (74%) 24-27 (22%)	Romero-Duque *et al.* (2007)
Jamaica (780mm, 5 mo.*, 27°C)	Clear-cutting (results for partial cutting treatment not shown)	Mean tree height Basal area Tree density Species density	10 (78%) 10 (35%) 10 (78%) 10 (84%)	Levesque *et al.* (2011)
Brazil (818 mm, 6 mo.*, 24°C)	Clear-cutting, fire, agriculture, pasture (?)	Mean tree height Mean tree basal area Mean tree density Mean tree species density	~26 (68%†) ~26 (69%†) ~26 (77%†) ~26 (94%†)	Madeira *et al.* (2009)
Puerto Rico (860 mm, 9 mo.*, 21.5°C)	Hurricane	Leaf area index Canopy cover Mean tree height	8 (90%) 8 (93%) 5.5 (34%)	Lugo *et al.* (2002)
Puerto Rico (860 mm, 9 mo.*, 21.5°C)	Urban (baseball park)	Species richness Species evenness Mean tree height Tree density Basal area Root biomass AGB	45 (85%) 45 (80%) 45 (59%) 45 (70%) 45 (42%) 45 (60%) 45 (16%)	Molina Colón (1998) cited in Lugo *et al.* (2002)
Puerto Rico (860 mm, 9 mo.*, 21.5°C)	Charcoal pits	Species richness Species evenness Mean tree height Tree density Basal area Root biomass AGB	45 (128%) 45 (100%) 45 (85%) 45 (114%) 45 (111%) 45 (89%) 45 (99%)	Molina Colón (1998) cited in Lugo *et al.* (2002)
Puerto Rico (860 mm, 9 mo.*, 21.5°C)	Clear-cutting, herbicide	AGB Leaf area index Species composition	13 (42%) 13 (64%) 13 (69%)	Murphy *et al.* (1995)
Mexico (900 mm, 6-7 mo., 26°C)	Agriculture	Tree density Canopy cover Canopy height Basal area Species density Shannon diversity Species evenness	8-13 (100%) 8-13 (100%) 13 (75%) 40 (60-89%) 40 (80-96%) 40 (86-90%) 40 (78-85%)	Lebrija-Trejos *et al.* (2008)
Dominican Republic (1000 mm, 6-7 mo., 25.5°C)	Clear-cutting, fire, agriculture, pasture, invasives	Species density	69 (100%)	Roth (1999)
India (1033 mm, 6-8 mo., 29.5°C)	Agriculture	Shannon diversity	~2 (27%†)	Kinhal and Parthasarathy (2008)

TABLE 1 (*Continued*)

Site and climate (P, dry months, T)	**Treatment or disturbance**	**Variable**	**Age in years (% recovery)**	**Reference**
Bolivia (1129 mm, 4 mo.*, 24.3°C)	Clear-cutting, fire, agriculture	Species richness Basal area Max. canopy height Tree density Canopy cover	5 (75%) 23 (75%) 20-40 (75%) 50 (200%) 5 (72%)	Kennard (2002)
Mexico (900-1400 mm, 6 mo.*, 25°C)	Agriculture	AGB	65-120 (100%)	Read and Lawrence (2003)
Mexico (1000-1500 mm, 8 mo.*, 26°C)	Clear-cutting, fire, agriculture, logging	Basal area	30-50 (70%)	Urquiza-Haas *et al.* (2007)
Lesser Antilles (1260 mm, 3 mo.*, 24°C)	Hurricane, drought	Tree density Tree mortality rate	6-8 (128%) <5 (100%)	Imbert and Portecop (2008)
Costa Rica (Palo Verde SDTF 1267-1717mm, 5 mo.*, 25°C) (Santa Rosa SDTF 1575mm, 6 mo.*, 25°C)	Clear-cutting, fire, agriculture	Tree density Shannon diversity	40-60 (100%) 40 (100%)	Powers *et al.* (2009)
Colombia (1584 mm, 4-5 mo., 27.6°C)	Clear-cutting, fire, agriculture, pasture (?)	Species density Basal area Mean tree height AGB	32-56 (82%) 32-56 (38%) 32-56 (86%) 30-50 (70%)	Ruiz *et al.* (2005)
Mexico (1650 mm, 4 mo., 24.2°C)	Hurricane or drought, fire	AGB BGB Total biomass AGC BGC Total carbon	80 (90%) 14 (90%) 70 (90%) 80 (90%) 18 (90%) 50 (90%)	Vargas *et al.* (2008)
India (1600-1800 mm, 4 mo.*, 25°C)	Logging	Shannon diversity Species evenness Mean tree density Basal area	~5-10 (86%) ~5-10 (84%) ~5-10 (91%) 6-8 (93%)	Saha (2003)

Abbreviations: AGB = Aboveground biomass; AGC = Aboveground carbon; BGB = Belowground biomass; BGC = Belowground carbon; mo. = months; P = Mean annual precipitation; T = Mean annual temperature.

2008). In any case, it appears the magnitudes of disturbances at these sites, sometimes chronic for more than a century, were insufficient to move the ecosystem out of the SDTF basin of attraction – a fact that attests to the importance of climatic and edaphic drivers and the presence of ecological memory. It remains unclear without further study whether or not such taxonomic or structural recovery translates to recovery of ecosystem functioning. Basal area may be similar to mature forests decades or centuries before maturity, whereas qualitative changes such as increases in stand-weighted wood density resulting from species composition changes occur more slowly (Brown and Lugo 1990). Similarly, recovery of species richness need not imply recovery of species composition (or vice versa, e.g. Lebrija-Trejos *et al.* 2008) and life-form abundance (e.g. Kupfer *et al.* 2004). As such, most studies of vegetation succession in SDTFs (~73%) have thus far focused on woody plants despite the majority of SDTF plants being non-woody (Quesada *et al.* 2009). Although it appears that species density recovers to mature forest levels faster than species composition does (Chazdon *et al.* 2007), it may be argued that the latter is less important to continued ecosystem functioning than the persistence of functional groups (Lugo *et al.* 2002, Quesada *et al.* 2009, Figure 2).

Quantitative measurement of SDTF ecological resilience, as defined in this review, has received lesser attention since it requires assessing the magnitude of disturbance the SDTF can absorb before shifting to an alternate state. Qualitatively, under intense disturbance such as frequent or high-intensity

TABLE 2 *Contribution of community characteristics and species functional traits to the resilience of SDTFs in the face of disturbance, based on evidence from published studies. A plus [+] in a cell indicates there is evidence from published studies (in the cited literature) that the increase in a community characteristic or trait prevalence* increases *the resilience (resistance, stability, or ecological resilience) of the community to the corresponding disturbance. Minuses [–] indicate* decreases*; solid circles [•] indicate that the characteristic or trait does not affect community resilience. For instance, there is evidence that the increase in prevalence of thick-barked species increases a community's resistance to fire. Similarly, increases in species diversity have been shown to both increase and decrease a community's resistance to invasion. Causation is from rows to columns, except when marked by a downward arrow [↓], when causation is from columns to rows. For example, land-use intensification has been shown to reduce functional response diversity. Upward triangles (Δ) signify characteristics (or traits) that have been shown in the literature to be higher (or more prevalent) in SDTFs, compared to MTFs. Downward triangles (∇) signify the opposite; circles (o) signify characteristics (or traits) that have not been shown in the literature to necessarily differ in these ecosystems. For example, compared to MTFs, SDTFs pass through fewer seral stages during succession, but have higher prevalence of obligately-outcrossing species. Citations prefixed with 'D' represent SDTF studies; those without the prefix come from other ecosystems and are largely made up of meta-analyses and reviews.*

	Disturbance →	**Unspecified / multiple**	**Drought / warming / shorter dry season**	**Fire**	**Invasives**	**Storms**	**Land-use change / resource extraction**
Community-level characteristics	Species diversity (∇[D7])	[+][1,10,11,14,15] [•][11,15] [–][11,15]	[+][2][•][3]		[+][3,4,5,D1] [–][4,5,D1]		[–][D2,D3] [•][D4] [•↓][17] [+↓][18] [–↓][18]
	Functional response diversity (Δ?[D42,D43])	[+][1,6,7,8,9]					[–↓][16]
	Nutrient-use efficiency (o[D8])				[+][D8]		
	Number of seral stages during succession (∇[D2,D5])						[–][D2,D3,D5]
	Structural complexity (∇[D6,D7,D8])						[–][D3, D6,D7,D8]
	Seasonality in reproduction (Δ)		[–][D52]				[–][D9,D10]
Species traits: Prevalence of species that…	… have specialized pollinators (Δ[D44,D45])	[–][D10]					[–][D9,D35]
	… are obligate outcrossers (Δ[D44,D10])	[–][D10]					[–][D9,D10,D11,D35] [+↓][D11]
	… are not animal dispersed (Δ[D9,D10,D13,D44,D45])	[+][D9,D13]		[+][D28]	[+][D38]		[+][D16,D39,D40,D41] [–][D39]
	… have short-lived seed banks (o[D7,D12,D14] Δ[D5,D13])						[–][D5,D7,D12,D13,D14]
	…have dormant / low-water content seeds (Δ[D13,D15,D16])						[+][D13,D15,D16]
	…have resprouting ability or invest in belowground reserves (Δ[D7,D46,D47,D48])	[+][12,13,D16,D17,D18, D19,D20,D27]		[+][D23,D25,D28,D31,D33,D49]	[+][D36]	[+][D30,37]	[+][D21,D22,D23,D24,D26,D29,D32]
	…have thick bark (Δ?[D34 compare D50])			[+][D19,D28,D31,D34,D50] [•][D33]			
	…have low growth rates and high structural investment in wood (Δ[D7,D8])					[+][D2,D37] [–][D30]	[–][D9]

TABLE 2 (*Continued*)

Disturbance →	**Unspecified / multiple**	**Drought / warming / shorter dry season**	**Fire**	**Invasives**	**Storms**	**Land-use change / resource extraction**
…have low P_{50} (pressure at which 50% of xylem hydraulic conductivity has been lost) (Δ?[D51])		[+][D51]				
…have low leaf water potential at turgor loss point (Δ?[D51])		[+][D51]				

[1] (Hooper *et al.* 2005) [2] (Mulder *et al.* 2001) [3] (Balvanera *et al.* 2006) [4] (Lonsdale 1999) [5] (Stohlgren *et al.* 1999) [6] (Elmqvist *et al.* 2003) [7] (Folke *et al.* 2004) [8] (Mori *et al.* 2013) [9] (Chapin *et al.* 1997) [10] (Loreau *et al.* 2001) [11] (Griffin *et al.* 2009) [12] (Bond and Midgley 2001) [13] (Vesk and Westoby 2004) [14] (Cardinale *et al.* 2013) [15] (Cottingham *et al.* 2001) [16] (Laliberté *et al.* 2010); includes northeastern Australian SDTF [17] (Carreño-Rocabado *et al.* 2012; references therein) [18] (Mayfield *et al.* 2010) [D1] (Brooks *et al.* 2013) [D2] (Ewel 1980) [D3] (Lebrija-Trejos *et al.* 2010) [D4] (Lebrija-Trejos *et al.* 2008) [D5] (Chazdon *et al.* 2007) [D6] (Ewel 1977) [D7] (Murphy and Lugo 1986) [D8] (Lugo *et al.* 2002) [D9] (Quesada *et al.* 2009) [D10] (Quesada *et al.* 2011) [D11] (Roth 1999) [D12] (Murphy *et al.* 1995) [D13] (Vieira and Scariot 2006) [D14] (Meave *et al.* 2012) [D15] (Gomez-Pompa *et al.* 1972) [D16] (Ceccon *et al.* 2006) [D17] (Brown and Lugo 1990) [D18] (Menaut *et al.* 1995) [D19] (Rundel and Boonpragob 1995) [D20] (Maass 1995) [D21] (Miller and Kauffman 1998) [D22] (Kammesheidt 1999) [D23] (Kennard *et al.* 2002) [D24] (González-Iturbe *et al.* 2002) [D25] (Saha and Howe 2003) [D26] (McLaren and McDonald 2003) [D27] (Sukumar *et al.* 2005) [D28] (Otterstrom *et al.* 2006; references therein) [D29] (Vieira *et al.* 2006) [D30] (Imbert and Portecop 2008) [D31] (Hoffmann *et al.* 2009) [D32] (Mostacedo *et al.* 2009) [D33] (Bunyavejchewin *et al.* 2011) [D34] (Pinard and Huffman 1997) [D35] (Ghazoul *et al.* 1998) [D36] (Ramaswami and Sukumar 2013) [D37] (Van Bloem *et al.* 2005) [D38] (Ramaswami and Sukumar 2011) [D39] (Teegalapalli *et al.* 2010) [D40] (Kupfer *et al.* 2004) [D41] (Klemens *et al.* 2011) [D42] (Medina 1995) [D43] (Hulshof *et al.* 2013) [D44] (Bullock 1995) [D45] (Gentry 1995) [D46] (Holbrook *et al.* 1995) [D47] (Martinez-Yrizar 1995) [D48] (Markesteijn and Poorter 2009) [D49] (Bowman *et al.* 2010) [D50] (Uhl and Kauffman 1990) [D51] (Chave 2014) [D52] (Bawa and Dayanandan 1998)

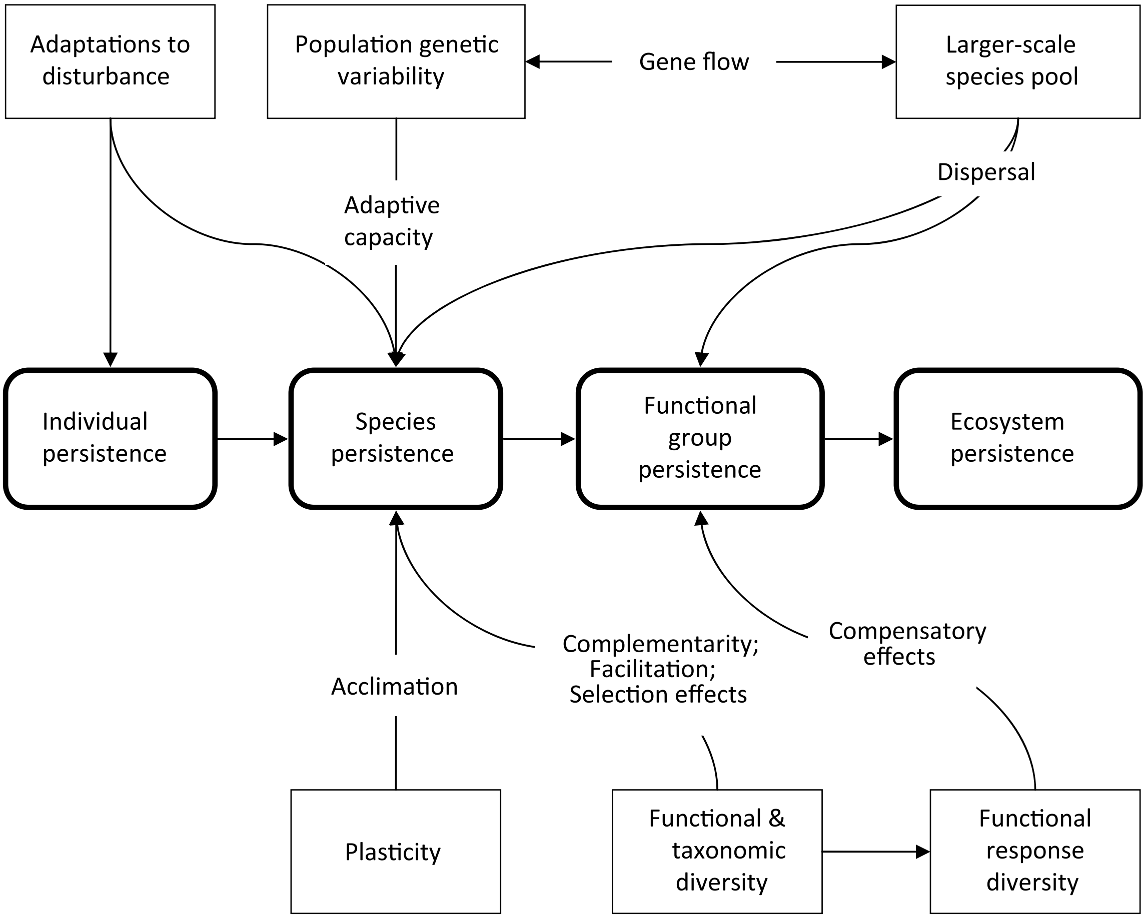
fires, clearing, prolonged drought, or species invasions, regime shifts to more open, scrub thicket, woodland, or savanna-like formations are predicted (Strang 1974, Blasco 1983, Murphy and Lugo 1986, Menaut *et al.* 1995, Miles *et al.* 2006, Lawrence *et al.* 2007, Ramesh *et al.* 2009a, Meir and Pennington 2011, Hoffmann *et al.* 2012). Many of such formations today are believed to be derived from disturbed SDTFs (Murphy and Lugo 1986, Roth 1999, Vieira and Scariot 2006, references therein, but see Saha 2003). Conversely, transitions to more closed, wetter formations may result from climatic changes or disturbances. As is discussed in the section on climate change, increased precipitation and/or atmospheric CO_2 in some regions may favor transitions of open formations to SDTF and SDTF to wetter forest types. Rare, catastrophic windstorms may result in significant compositional shifts: such an event is believed to have killed most vegetation in an area of approximately 500ha during the early- to mid-1800s in an SDTF in Thailand, and possibly resulted in a shift from a deciduous forest type to an evergreen forest type (Bunyavejchewin *et al.* 2011). Although such events appear to be rare, the intensity – greater peak wind speeds and heavier precipitation – of tropical storms (including hurricanes) is predicted to increase as a result of climate change (IPCC 2007) and it remains unclear what impacts such a change is likely to have on SDTFs.

Some disturbances facilitate others: for example, invasion often accompanies SDTF degradation or conversion to other land uses (e.g. Fensham 1996, Roth 1999, Molina Colón and Lugo 2006, Romero-Duque *et al.* 2007, Veldman *et al.* 2009, Veldman and Putz 2010). Similarly, localized contraction of northern Australian SDTFs during the late Holocene has been attributed to the combined effect storms and subsequent fires occurring in storm debris (Bowman *et al.* 1999). Positive feedbacks between invasive plants, especially grasses, and fire or nutrient cycling can reduce SDTF resilience, potentially leading to regime shifts (D'Antonio and Vitousek 1992, Johnson and Wedin 1997, Brooks *et al.* 2004, Hiremath and Sundaram 2005, Veldman *et al.* 2009, Laurance *et al.* 2011). In some cases, recovery of pre-invasion SDTF structure and function may be impossible without long-term management (Brooks *et al.* 2004, Cordell and Sandquist 2008, Ammondt *et al.* 2013).

Studies of community-level characteristics or species functional traits relevant to SDTF resilience

Several studies (Table 2) suggest that the smaller species pool size, shorter-statured and simpler vegetation structure, and fewer seral stages during succession (possibly owing to greater resprouting ability) of SDTFs, when compared

FIGURE 2 *Factors influencing the persistence of ecosystems.*



to MTFs, can promote quicker convergence of primary and secondary vegetation following severe disturbances. These expectations have been contested (Quesada *et al.* 2009) and indeed, not only do recovery-time estimates vary considerably across SDTFs (Table 1), but whether SDTFs may be considered more or less stable than MTFs depends considerably on the variable used to measure recovery (e.g. Opler *et al.* 1977, Murphy and Lugo 1986, Kennard 2002, Van Bloem *et al.* 2005, Lebrija-Trejos *et al.* 2008, Imbert and Portecop 2008). In addition, within SDTFs, there appears to be no obvious relationship between recovery time and site annual precipitation (Table 1). These differences are partly due to differences in disturbance regime but also due, no doubt, to the heterogeneous nature of SDTFs. The long-term successional studies in subtropical dry and wet forests of Puerto Rico (Lugo *et al.* 2002) are instructive because these forests had similar disturbance regimes and biotemperatures, and occurred within the same latitudinal belt. Lugo *et al.* (2002) concluded that as more variables are evaluated over longer time scales, both forests appeared to be equally stable. While more such comparative studies are needed, the only conclusion that can be drawn at this point is that globally, SDTFs are, on average, just as vulnerable as MTFs. This general statement can then be qualified further in the context of a particular region and/or disturbance regime. The studies cited in Table 2 suggest that SDTFs are likely to be less resilient than MTFs to some disturbances (loss of specialist pollinators) than to others (loss of animal dispersers resulting from land-use change or resource extraction, fires, and drought); for still others (invasion, storms, land-use change), neither forest type is necessarily more resilient. These ideas are discussed in some detail in the remainder of this section.

The loss of specialist pollinators will presumably impact a greater fraction of species in most SDTFs, compared to MTFs, because of the greater fraction of obligate outcrossers and species with specialist pollinators (references in Table 2). Genetic diversity – maintained by pollen and seed dispersal – is an important component of resilience as it determines the adaptive capacity of species (Figure 2). Changes to microclimate (increased evapotranspiration and temperature and drier soils) resulting from forest degradation can affect SDTF plant phenology, reducing leaf life span and triggering earlier flowering (Quesada *et al.* 2011). Quesada *et al.* (2009) suggest that because many SDTF pollinators depend on sequential flowering, changes in flowering phenology, and particularly synchrony, during succession can affect genetic relatedness, reproductive output, and even mating patterns of plants, which can impact genetic diversity. In addition, habitat fragmentation is known to significantly decrease pollination, reproductive output, and allelic richness in tropical plant populations (Quesada *et al.* 2011). Thus, SDTF plant populations in fragmented or degraded landscapes may be at particular risk, lacking the capacity to adapt to rapid climate change.

Loss or reduction of animal dispersers due to hunting or habitat fragmentation will presumably impact the reproductive success of a smaller fraction of species in most SDTFs, compared to most MTFs, because of the greater fraction of wind-dispersed species (references in Table 2). This is certainly true of early successional stages that tend to be dominated by wind-dispersed species (Opler *et al.* 1980, Powers *et al.* 2009, Lohbeck *et al.* 2013). Similarly, comparisons of stem and leaf traits that are sensitive to water stress suggest that a smaller fraction of SDTF species may be at risk of drought-induced mortality compared to MTFs – it is unclear whether or not greater species richness in MTFs would allow ecosystem functioning to be maintained by compensatory effects, facilitation, or selection effects (Mulder *et al.* 2001, Balvanera *et al.* 2006, Chave 2014). It is clear from Table 2 that a globally-convergent feature of SDTFs is the prevalence of the ability to resprout, which is key to recovery from a variety of disturbances including fire, drought, logging, storms, invasion, herbivory, and landslides. Possibly because of established root systems and carbohydrate reserves, resprouts usually have greater sizes and higher survival than seedlings, although growth rates may be comparable (Miller and Kauffman 1998, Kennard *et al.* 2002, Mostacedo *et al.* 2009). However, the role of resprouting ability in increasing SDTF resilience needs further qualification with respect to disturbance regime. Anthropogenic disturbances such as cultivation may result in compositional shifts towards species with resprouting ability if external propagules are lacking (Roth 1999, González-Iturbe *et al.* 2002). Repeated topkill due to high fire frequencies, repeated clearing, or cultivation involving intensive tractor use can result in the loss of resprouting ability (Vieira and Scariot 2006, Timberlake *et al.* 2010) or depletion of belowground reserves, eventually leading to plant mortality (Bond and Midgley 2001). High-intensity fires, such as those resulting from fuel-load buildup resulting to long-term fire suppression (Stott 1986, Wanthongchai and Goldammer 2011), or severe anthropogenic disturbances (e.g. house building, ploughing) can kill or damage belowground tissues of sprouting individuals and deplete the density of viable seeds (Kennard *et al.* 2002, Molina Colón and Lugo 2006, Madeira *et al.* 2009). In such cases, internal ecological memory, as defined previously, is erased and SDTF recovery contingent on external ecological memory in terms of seed sources in the surrounding landscape (e.g. Lugo *et al.* 2002, Molina Colón and Lugo 2006, Madeira *et al.* 2009).

Traits such as serotiny that are clear fire adaptations (Bond and Midgley 2001) have not been documented for woody plants in SDTFs and bark thickness of SDTF species, although greater than that of MTF species, is considerably lesser than that of fire-tolerant savanna species (references in Table 2). Although natural, lightning-caused fires can occur in SDTFs (Keeley and Bond 2001), actual recorded incidences of such fires appear to be extremely rare in the literature (e.g. Lowrie 1891, Middleton *et al.* 1997). By contrast, for example, ground lightning-flash density in some grassland and savanna ecosystems of South Africa is approximately 1-10 km^{-2}yr^{-1} (van Wilgen *et al.* 2000), translating to large areas being subsequently burnt (Edwards 1984). Whatever their causes in the past, fires in SDTFs today are believed to largely be anthropogenic in origin (Murphy and Lugo 1986, Timberlake *et al.* 2010, McShea and Davies 2011, Wanthongchai and Goldammer 2011, Sanchez-Azofeifa and Portillo-Quintero 2011), which has led to the question of whether or not woody plants in SDTFs are adapted to present fire regimes. Periods of fire exclusion appear to promote SDTF expansion into adjacent open formations such as savanna (Bowman and Fensham 1991). It has been suggested that woody plants from the drier tropics may have a certain degree of "pre-adaptation" to fires due to greater relative investment in belowground reserves and greater resprouting ability – possibly adaptations to other disturbances such as drought or large-mammal herbivory (Bond and Midgley 2001, 2003) – compared to species from the wetter tropics (Hoffmann *et al.* 2009). However, SDTFs in northern Australia, which are embedded within a fire-tolerant, Eucalypt-dominated savanna landscape, are fire sensitive and tend to occur in topographic positions that are protected from fire (Andersen *et al.* 2005). The composition of woody plant species seen in most SDTFs today is likely a result of selection for species that have been able to persist through disturbances such as droughts and fire (Swaine 1992, Hoffmann 1998, Saha and Howe 2003, Otterstrom *et al.* 2006, Vieira *et al.* 2006). Although Australian SDTFs are relatively fire sensitive – and obligate-seeder species appear to particularly susceptible, most species can recover following a single fire (Bowman *et al.* 2010). Some SDTFs may be secondary or successional formations resulting from disturbances such as fire (Pascal 1986, Murphy and Lugo 1986). Whether or not exclusively adapted to fire, woody plant communities in many SDTFs appear to be resilient to infrequent, low- to medium-intensity understorey fires. Higher fire frequencies or higher-intensity fires can reduce SDTF resilience by depleting soil nutrients (Wanthongchai and Goldammer 2011) and, as discussed previously, by killing or damaging belowground plant tissues, reducing resprouting ability, depleting viable-seed densities, and depleting belowground plant reserves, resulting in plant mortality.

Few studies have specifically addressed SDTF resilience in the face of alien invasion (but see Lugo *et al.* 2002). Invasive impacts on native SDTF species include direct effects such as competition for abiotic and biotic resources (Ghazoul 2004, Cordell and Sandquist 2008, Heleno *et al.* 2013, 2013, reviewed in Traveset and Richardson 2006, Kaiser-Bunbury *et al.* 2010) and indirect effects such as alteration of soil nutrient cycling (Litton *et al.* 2006, 2008, reviewed in Ehrenfeld 2003). However, invasive plants can also facilitate regeneration and growth of native SDTF species (Romero-Duque *et al.* 2007, references therein). Invasion resistance may be increased when natives are better able to utilize resources, either through complementarity or sampling effects. Invasion resistance may therefore be enhanced by high nutrient-use efficiency, which can also decrease nutrient losses, thereby increasing ecosystem resilience (Lugo *et al.* 2002). Nutrient-use efficiencies in SDTFs and MTFs appear to be comparable (Murphy and Lugo 1986, Lugo *et al.* 2002), though additional studies are needed. As in the case of fire, certain traits could make SDTF species "pre-adapted" to invasive-induced environment changes. For example, resprouting ability in woody-plant seedlings has been speculated to be a mechanism for their persistence even under high densities of an invasive shrub in an SDTF in India (Ramaswami and Sukumar 2013).

There is now considerable theoretical and some empirical support for the idea that higher biodiversity can lead to greater ecosystem resilience (Hooper *et al.* 2005, Balvanera *et al.* 2006, Griffin *et al.* 2009). The major mechanisms involved are illustrated in Figure 2. Because few studies have explicitly examined the relationship between biodiversity and SDTF resilience, studies from other ecosystems are instructive and are summarized in the first two rows of Table 2. These studies suggest that (a) ecosystem resilience does, on average, increase with biodiversity, (b) some biodiversity measures, such as functional response diversity, are more consistent indicators of ecosystem resilience than measures such as species richness (because species identities matter), (c) resilience can be eroded (even as an ecosystem appears resistant to disturbances): disturbances such as land-use intensification can affect (increase or decrease) both the species richness and functional diversity of an ecosystem, but changes in the two measures may not be positively correlated except in cases such as when sampling effects are active (Mayfield *et al.* 2010), and (d) resilience can be regained after the disturbance has been removed: functional diversity can increase during succession (e.g. Lohbeck *et al.* 2012). While the generality of such results is far from established, the congruence of some results across multiple biomes and biogeographic zones suggests their applicability to SDTFs. Thus, despite the relatively low woody-plant diversity in SDTFs, high dispersion of Specific Leaf Area (SLA) and wood density in the cited studies (Table 2) may increase SDTF resilience to some disturbances, compared to MTFs; whether this functional diversity translates to response diversity within functional effect groups needs investigation, the latter having a more direct link to ecosystem resilience (Mori *et al.* 2013).

The major challenge for future studies lies in predicting the net response of SDTFs to multiple, potentially-interacting disturbances whose effects can be cascading or canceling (Dale 2011). For example, the impact of land-use/cover modification may have to be examined in conjunction with increasing atmospheric CO_2 and temperature, and a changing rainfall regime. This is an inherently difficult proposition, and moving beyond qualitative assessments that are based on expert knowledge requires modeling of SDTF dynamics as is discussed in the subsequent section in the context of global change. Parameterization of such models once again calls for data from long-term studies.

GLOBAL CHANGE

Modeling SDTF dynamics

The impact of global change on SDTFs may be in the form of distributional and compositional shifts (which subsume SDTF degradation and conversions between SDTF and other vegetation types) and is the outcome of the fundamental processes of survival, growth, fecundity, and dispersal of individuals. These processes may be modeled based on knowledge of the physiological tolerances, dispersal abilities, and biotic interactions of constituent species. Such information, however, is typically unavailable for most species, necessitating model simplification. Consequently, the impacts of global change on SDTFs have been studied using models of varying degrees of complexity, reflecting the dual tradeoffs of realism vs. tractability and generality vs. specificity (Thuiller *et al.* 2008). Dynamic Global Vegetation Models (DGVMs) typically operate on a small number of Plant Functional Types (PFTs) and are able to broadly predict vegetation patterns at a global scale. At the other extreme, individual-based models (IBMs) simulate the dynamics of each individual plant, leading to emergent ecosystem-level predictions. Hybrids of the two approaches also exist (e.g. Sato *et al.* 2007). Finally, species distribution models (SDMs) relate biotic and abiotic factors with species distributions, without necessarily being mechanistic (Kearney and Porter 2009).

Nutrient alteration

Highly weathered soils depleted of phosphorous (P) in tropical forests make vegetation reliant on atmospheric P deposition via rain, fog, and dust (DeLonge et al 2008). Such deposition may come from local sources (e.g. slash-and-burn agriculture) or long-range dust transport. The ability of forest canopies to trap dust and fog water and the subsequent transfer of nutrients to the ground via throughfall and stemflow (Das *et al.* 2011), potentially results in a positive feedback between P deposition and vegetation. SDTFs may be more reliant on P inputs from fog and dry deposition compared to MTFs, due to their lower rainfall. In such cases, reduction of atmospheric P inputs or loss of canopy cover may reduce the resilience of SDTF to the point that relatively small disturbances may result in a regime shift to open-canopied or treeless formations (DeLonge *et al.* 2008). After multiple cycles of shifting cultivation, P loss (due to leaching, burning, and harvest) and subsequent reduction of P inputs due to the positive feedback between canopy cover or forest age and atmospheric P deposition can slow down, or even prevent, SDTF recovery (Lawrence *et al.* 2007).

Climate change

SDTF responses to past climate change

Meir and Pennington (2011) reviewed evidence from paleo- and recent historical studies, which support the idea that neotropical SDTFs are strongly drought tolerant; SDTF trees are able tolerate several years of suboptimal growth, and

SDTF populations in parts of Peru and Bolivia have been stable for up to 10 million years in small geographic regions through the drier climates of the Pleistocene. It has further been suggested that SDTFs were more extensive during glacial periods, which were drier, cooler, and had lower atmospheric CO_2 compared to the present, and that this expansion involved smooth changes in floristic composition as opposed to abrupt regime shifts (Pennington *et al.* 2009, Linares-Palomino *et al.* 2011, Chave 2014) On the other hand, SDTFs in north eastern Australia are rarely found in regions with mean annual rainfall less than 500mm, and it has been suggested that SDTF would have retreated to a few refugia during the Pleistocene (Fensham 1995).

Responses of SDTF species

Interannual variability in climate, and particularly precipitation, through its impact on plant water status, is known to be an important driver of woody plant growth and survival in SDTFs. Although a variety of factors may predispose an individual plant to drought-induced mortality regardless of species (e.g. site characteristics, age, size), there is considerable inter-specific variation in drought responses of SDTF plants that is governed by traits such as rooting architecture and depth, wood density, leaf lifespan, and stem water storage (Holbrook *et al.* 1995, Meir and Pennington 2011). In SDTFs, compositional shifts towards slow-growing species with conservative water-use strategies may be favored (Craven *et al.* 2013).

The effects increasing water stress and rising CO_2 on the physiology of tropical forest trees are debated (e.g. Lloyd and Farquhar 2008). Increasing temperature is expected to increase leaf-to-air vapor pressure deficits, enhancing transpiration. The resulting soil water deficits may be compounded if there is also a decrease in precipitation. In response, SDTF plants can achieve water-loss limitation by increased stomatal closure, increasing intrinsic water-use efficiency (Brienen *et al.* 2011, Craven *et al.* 2013) and decreasing productivity (Malhi *et al.* 2009). However, increasing CO_2 diffusion is expected to enhance productivity. Under experimental conditions, short-term exposure of SDTF tree seedlings to elevated CO_2 has shown up to 1012% increase in leaf area and 460% increase in biomass depending on species (Khurana and Singh 2001). This effect may – to a small extent – also be counteracted by increasing temperature because forest leaves are optimized to operate at the current temperature (Lloyd and Farquhar 2008). Brienen *et al.* (2011) reported a 40% increase in intrinsic water use efficiency during the last four decades in an SDTF tree, the cause of which was attributed to a reduction in stomatal conductance in response to CO_2 increase, implying that photosynthetic rates were unlikely to have changed. Increasing CO_2 is also likely to favor C_3 plants (most trees) over C_4 plants (grasses), favoring shifts to forest at forest-savanna ecotones (Malhi *et al.* 2009). Liana growth is likely to respond faster to atmospheric CO_2 enrichment compared to trees, especially in seasonal forests (Schnitzer and Bongers 2011). A 30% increase in liana abundance during the last decade was reported from a tropical dry evergreen forest in India; however it was accompanied by 30% decrease in tree density attributed to anthropogenic disturbance, suggesting that future liana spread may be checked by a lack of host trees at these sites (Baithalu *et al.* 2013, Pandian and Parthasarathy 2013).

Strong seasonality in reproduction makes many SDTF species vulnerable to changes in seasonal precipitation patterns, which can affect flowering and fruiting phenology. A shortening dry season can increase the temporal overlap of flowering individuals belonging to different species, potentially intensifying competition for shared pollinators and clogging stigmas with heterospecific pollen grains, thereby reducing reproductive output (Bawa and Dayanandan 1998).

Responses of individual SDTF species depend not only on abiotic factors but also community-level changes because a forest's canopy modifies local microclimate and atmospheric nutrient deposition, thereby affecting fire risk, humidity, and the availability of soil moisture, light, and nutrients (e.g. DeLonge *et al.* 2008, Lebrija-Trejos *et al.* 2011, Hoffmann *et al.* 2012).

Interaction of climate change with other drivers

Plant water stress is exacerbated at higher temperatures through increased evapotranspiration, and can, in turn make plants more vulnerable to other agents of mortality such as biotic attacks and dry-season fires (McDowell *et al.* 2008, Adams *et al.* 2009, Allen *et al.* 2010). In general, increasing temperature and reduced precipitation have been predicted to result in more severe fire weather, greater area burned, more ignitions, a longer fire season, and increased forest susceptibility to fire (Dale *et al.* 2001, Wanthongchai and Goldammer 2011). Widespread land-use change and fires are in turn expected to reduce regional precipitation (Meir and Pennington 2011). Severe fires in SDTFs are expected to exacerbate nutrient loss, soil erosion, and landslides (Wanthongchai and Goldammer 2011).

The impact of climate change on invasives could be both positive and detrimental. For instance, the ranges of four species of invasive grasses in tropical Australia were predicted to decrease under the A2a emissions scenario of climate change under all global climate change models used in the study (Gallagher *et al.* 2013). By contrast, under experimental conditions, CO_2 enrichment was found to increase the physiological performance of two common invasive plants in SDTFs of India over that of native woody plants (Raizada *et al.* 2009).

Predicted SDTF distribution

Incorporation of the processes outlined in the previous two sections (i.e. plant physiological processes and interactions between multiple drivers) into models of global change in a computationally efficient manner remains a challenge (Meir and Pennington 2011). The predictions presented in this section represent model simplifications to various degrees.

At a global scale, Miles *et al.* (2006) estimated that a far greater proportion (>35%) of SDTFs in the neotropics were at risk from severe climate change (defined by the authors as temperature increase of at least 2.5°C or precipitation decrease of at least 50mm/yr) – reflecting the large predicted decreases in precipitation under a "business as usual scenario" (IS98a) – compared with other SDTF regions (<20%). Collevatti *et al.* (2013) used SDM ensemble simulation for sixteen Brazilian SDTF species and reported similar patterns of climatic habitat suitability between the Last Glacial Maximum and the present but significant reduction and shifts of suitable SDTF habitats by the end of the 21st century. The climatically-stable regions suitable for each of the sixteen species matched with at least one reserve in Brazil and yet, it was predicted that most species would be lost from protected areas and may be unable to track the changing climate in a fragmented landscape. Chaturvedi *et al.* (2010) used the DGVM approach to predict that over 40% of SDTF grids in India would become climatically suitable for wetter forest types under the A2 and B2 emissions scenarios, with an overall trend of potential shifts towards wetter vegetation types.

It is possible that new areas may become climatically suitable for SDTF. For example, Malhi *et al.* (2009) suggested that increased dry-season water stress in eastern Amazonian rainforest during the 21st century under the A2 emissions scenario would support transition to SDTF rather than savanna due to the predicted annual rainfall regime. As outlined previously, increasing CO_2 can, to an extent, counteract drying by increasing water-use efficiency (Malhi *et al.* 2009). The upshot of these effects combined was predicted to result in an overall increase in evapotranspiration that would in turn increase the threshold annual rainfall needed to support SDTF instead of savanna. Malhi *et al.* (2009) argued that land-use change and intensification increase fire risk, reducing any inherent resilience of the forest to dry-season intensification and triggering transition to low-biomass forests. Meir and Pennington (2011) suggest that Amazonian rainforest soils typically are nutrient poor making transition to SDTF unlikely; instead shifts to the transitional ecotone between rainforest and savanna or savanna itself may be favored, depending on the strength of drying and fire frequencies. Similarly, Chaturvedi *et al.* (2010) predicted that large areas of savanna and grassland grids in India may become climatically suitable for SDTF, although it remains unclear whether or such sites will be sufficiently nutrient rich to support SDTF.

Expansion of fire-sensitive northern Australian SDTFs into Eucalypt-dominated savanna since the mid-20th century has been extensively documented (e.g. Russell-Smith *et al.* 2004, Banfai and Bowman 2006). In some regions, this expansion is hypothesized to be driven by increases in both regional precipitation and global atmospheric CO_2, despite a post-Aboriginal fire regime involving intense fires (Banfai and Bowman 2006, 2007, Bowman *et al.* 2010). In others, SDTF expansion has been attributed to release from burning pressure following the disruption of Aboriginal practice of setting frequent, low-intensity fires (Russell-Smith *et al.* 2004). Banfai and Bowman (2006) ranked the relative importance of interactions between rainfall, CO_2, fire, invasive plants and feral animals on SDTF-savanna dynamics in Kakadu National Park, northern Australia, based on available evidence that included long-term data spanning four decades. They suggested that the strongest driver of SDTF expansion in the region was increasing rainfall, followed by increasing CO_2, which also potentially allowed C_3 SDTF plants to grow fast enough to escape recurrent fires. The strongest driver of SDTF contraction, where it occurred, was hypothesized to be increasing fire frequency and/or intensity. Weaker drivers included invasive-plant expansion and higher rainfall, which tended to increase fire frequency and intensity by increasing fuel loads, and increases in the abundance of feral animals, which had the opposite effect. SDTF expansion at the expense of savanna is predicted to continue under current climatic trends and management practices (Banfai and Bowman 2007).

SYNTHESIS

SDTF is a heterogeneous set of forests that occur in the seasonal tropics in regions that are presently characterized by low-rainfall conditions. Within a climatic regime, they frequently co-occur with open formations such as savanna, and boundary fluctuations between the two, mediated by factors such as fire regime and soil-nutrient status, at timescales as small as a few decades may be considered a part of the natural dynamic of this ecosystem. Moisture availability is an important control of woody biomass and there is evidence that temporal variation in precipitation and temperature has driven SDTF expansion and contraction at timescales ranging from decennial to millennial. Such transitions include smooth changes in floristic composition as well as abrupt regime shifts when positive feedbacks are involved, such as those between grass cover and fire, or tree cover and atmospheric P inputs. SDTF response to global and local anthropogenically-driven change is superimposed on this background natural variation.

SDTF plant species life histories have been shaped by endogenous drivers including climatic fluctuations, herbivory, and in some cases, fire and storms. Where the drivers are exogenous (e.g. modified fire regimes, resource extraction, land-use change, alien invasion), and have not been active on evolutionary timescales, SDTF species may still possess traits (primarily the ability to resprout after disturbance and invest in belowground reserves) that make them "pre-adapted" to such conditions. There is evidence that some SDTF biodiversity- and structure-related properties are resistant to low- to moderate-intensity disturbances.

When a severe pulse or chronic disturbance ends (e.g. abandoned field following shifting agriculture, logging, fire, hurricane, drought), the successional process in SDTFs appears to restore structural and taxonomic attributes such as above- and below-ground biomass, stem density, canopy cover and height, and species composition and richness, at timescales in the order of decades. However, it is unclear whether or not ecosystem functioning takes longer to recover. If a disturbance remains chronic (e.g. repeated fires or clear-felling, changes in climate, change in atmospheric nutrient inputs, alien invasion), ecological memory – internal or external – may be erased, soil nutrients depleted, and functional composition altered. Chronic fire and anthropogenic disturbances are believed to already have altered the structure and species composition of some SDTFs. With the erasure of internal ecological memory (e.g. stumps and root stocks, soil seed bank) recovery may still be possible if external propagule sources from the surrounding landscape matrix are present. If natural succession is impeded due to loss of ecological memory or nutrient alteration, regime shifts to alternate domains of attraction are predicted. Typically, these are predicted to be more open formations physiognomically resembling scrub thicket, savanna, grassland, or woodland but containing SDTF elements. Such regime shifts may be precipitated by positive feedbacks or interactions between drivers such as fire, invasives, storms, land-use change, atmospheric nutrient deposition and climate change.

Although it was originally believed that SDTFs are inherently more stable than MTFs, recent studies suggest that globally, SDTFs are, on average, just as stable. Different SDTF community variables (e.g. biomass, species richness) recover at different rates compared to MTF counterparts, and furthermore, recovery rates depend on the nature of disturbance. Based on examination of community-level characteristics and species functional traits, it is suggested that SDTFs may be more resilient than MTFs to certain kinds of disturbances (fires, drought, and loss of animal dispersers) than to others (loss of pollinators). Variation of some functional traits in SDTFs exceeds that of MTFs hinting at the possibility of higher response diversity, and therefore resilience to some disturbances, although this needs be tested and the generality of this trend with respect to other traits examined.

There is considerable uncertainty in the predicted response of SDTFs to future changes in climate interacting with other, largely anthropogenic, drivers. Increasing atmospheric CO_2 and temperature, and changes in total and seasonal precipitation, could have reinforcing or canceling effects on the physiology of SDTF plants, leading to changes in their growth, survival, and reproductive output. While some SDTF sites are likely to continue to remain climatically suitable for most constituent species, in others, precipitation regimes may no longer be able to support SDTF. Depending on regional precipitation patterns, areas presently containing other ecosystems (e.g. rainforests in Brazil, grasslands or savannas in India and northern Australia) may be become climatically suitable for SDTFs, although vegetation change is likely to be mediated by edaphic factors and in some regions, accelerated by resource extraction and the concomitant increase in fire risk. Wherever climatically suitable areas shift in space, SDTF species will need to disperse through a fragmented landscape, potentially outside reserves, as they track the shifting climatic envelope.

More regional and landscape-specific studies of SDTF are needed in order to identify globally convergent SDTF responses to various disturbances. In particular, there is a need for more paleoecological studies and long-term studies in relatively undisturbed SDTF to help establish baseline dynamics against which the effects of modified or novel disturbance regimes can be assessed. Comparisons of ecosystem resilience between SDTFs and other vegetation types will benefit from studies that control for other factors, such as latitude and disturbance regime. Quantitative prediction of SDTF responses to multiple, potentially interacting drivers remains a challenge – particularly when feedbacks between drivers are known to exist – and requires modeling of SDTF dynamics, which, again, can benefit from data from long-term studies.

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