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Succession and management of tropical dry forests in the Americas: Review and new perspectives

Mauricio Quesada [a,*], G. Arturo Sanchez-Azofeifa [b], Mariana Alvarez-Añorve [a], Kathryn E. Stoner [a], Luis Avila-Cabadilla [a], Julio Calvo-Alvarado [c], Alicia Castillo [a], Mario M. Espírito-Santo [d], Marcilio Fagundes [d], Geraldo W. Fernandes [e], John Gamon [b], Martha Lopezaraiza-Mikel [a], Deborah Lawrence [f], Leonor Patricia Cerdeira Morellato [g], Jennifer S. Powers [h], Frederico de S. Neves [d], Victor Rosas-Guerrero [a], Roberto Sayago [a], Gumersindo Sanchez-Montoya [a]

[a] *Centro de Investigaciones en Ecosistemas, Universidad Nacional Autonoma de Mexico, Apartado Postal 27-3 (Xangari), Morelia, Michoacan 58089, Mexico*
[b] *Earth and Atmospheric Sciences Department, University of Alberta, Edmonton, Alberta, Canada*
[c] *Escuela de Ingenieria Forestal, Instituto Tecnologico de Costa Rica, Cartago, Costa Rica*
[d] *Departamento de Biologia Geral/CCBS, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais, Brazil*
[e] *Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil*
[f] *Department of Environmental Sciences, University of Virginia, Charlottesville, VA, USA*
[g] *Departamento de Botânica, IB – UNESP, Universidade Estadual Paulista, Sao Paulo, Brazil*
[h] *Departments of Plant Biology, Ecology, Evolution and Behavior, and Soil, Water and Climate, University of Minnesota, St. Paul, MN, USA*

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ABSTRACT

Understanding tropical forest succession is critical for the development of tropical forest conservation strategies worldwide, given that tropical secondary forests can be considered the forests of the future. Tropical dry forests (TDF) are among the most threatened tropical ecosystems, there are more secondary forests and forest restoration efforts that require a better understanding of successional processes. The main goal of this synthesis for this special issue on the ecology and management of tropical dry forests in the Americas is to present a summarized review of the current knowledge of the ecology and management implications associated to TDF succession. We explore specific issues associated to tropical dry forest succession with emphasis on the use of chronosequences, plant diversity and composition, plant phenology and remote sensing, pollination, and animal–plant interactions; all under the integrating umbrella of ecosystem succession. We also emphasize the need to conduct socio-ecological research to understand changes in land-use history and its effects on succession and forest regeneration of TDF. We close this paper with some thoughts and ideas associated with the strong need for an integrating dimension not considered until today: the role of cyberinfrastructure and eco-informatics as a tool to support sound conservation, management and understanding of TDF in the Americas.

1. Introduction

Understanding tropical forest succession is critical for the development of tropical forest conservation strategies worldwide, given that tropical secondary forests can be considered the forests of the future (Wright, 2005; Sanchez-Azofeifa et al., 2005). Past and present rates of tropical land conversion clearly indicate that most mature tropical forests will eventually disappear leaving behind a complex landscape consisting of a matrix of agricultural fields and forest patches under different levels of succession. This is particularly the case of tropical dry forests (TDF) that remain currently exposed to several threats resulting from human activity (Sanchez-Azofeifa et al., 2005; Miles et al., 2006). Understanding tropical succession in the context of different ecological and human dimensions represents one of the key present challenges to promote and develop conservation and management programs for this threatened ecosystem.

The land cover matrix in the tropics is composed of an astonishing diversity of life forms and species that have been shaped by natural selection and biotic and abiotic factors associated with a wide variety of different habitats. Tropical rainforests are just one of them, but our fascination with their extent and high number of species have driven the forces that contribute to our understanding of tropical ecology. We claim that

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* Corresponding author.
E-mail address: mquesada@oikos.unam.mx (M. Quesada).

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many other vegetation formations, some of large extension such as savannas and dry forests, constitute other regions of major biological importance but are much less understood.

Approximately 42% of tropical forests around the world are TDF (Murphy and Lugo, 1986; Miles et al., 2006), although most knowledge in tropical forest succession has been obtained from rain forest plant communities (Vieira and Scariot, 2006). A search on the ISI Web of Science database from 1900 until March 2009 for articles with the words "succession", and "tropic*" in the title and summary, indicate a great difference in the number of studies conducted in each ecosystem (436 in "rain forest" vs. 60 papers in "dry forest"). In addition, TDF have been extensively transformed and occupied by urban and agricultural areas at significantly higher rates than tropical rainforests (Murphy and Lugo, 1986). For example, just in Latin America alone, approximately 66% of TDF have already been destroyed (Portillo, personal communication). Hence, we must better understand the ecology of succession and the effects of forest management programs on these other equally important ecosystem around the world.

A review of dry tropical forest ecology originally predicted that this ecosystem was likely to recover more quickly to a mature state than do wet forests because of the relative simplicity and small structure of mature forests, and the predominance of coppicing after disturbance (Ewel, 1977; Murphy and Lugo, 1986; Segura et al., 2003). However, these interpretations have been based on speculations with very little empirical evidence. If succession is a slower process in tropical dry than rainforests, in terms of plant growth and other developmental features (Ewel, 1977; Murphy and Lugo, 1986), it is contradictory to expect faster rates of succession for TDF. Apparently, coppicing from stumps and roots remaining after disturbance is expected to take less time to reach maturity and it is considered as the primary regeneration mechanism of disturbed tropical dry sites (Ewel, 1977; Murphy and Lugo, 1986). However, a review of plant sexual expression and mating systems of TDF indicates that the predominant mode of reproduction is through a wide variety of sexual systems where seeds are mainly produced via outcrossing (Quesada et al., in press). Under clonal asexual reproduction (as suggested through coppicing) we should expect low genetic variation in tree populations; however, evidence shows high genetic diversity among adult tree populations that can only be attributable to sexual reproduction via seed dispersal and seedling regeneration (Hamrick and Loveless, 1986; James et al., 1998; Quesada et al., 2004, in press).

Janzen (1988) stated that restoration of dry forest pastures might follow two different patterns, occurring at the same time: one controlled by wind-dispersed tree seeds and another controlled by seeds defecated by animals. Therefore, it is unlikely that ecological succession of TDF is a process that reaches a mature state relatively fast as suggested above by several authors. In fact, it has been proposed that TDF should be even more susceptible to human disturbance because growth rate and regeneration of plants is slow, reproduction is highly seasonal and most plants are mainly outcrossed and dependent on animal pollination (Bawa, 1974, 1990; Frankie et al., 1974; Murphy and Lugo, 1986; Hamrick and Murawski, 1990; Bullock, 1995; Jaimes and Ramirez, 1999; Quesada et al., 2001, 2004, in press; Cascante et al., 2002; Fuchs et al., 2003).

More recently, it has been proposed that seasonality and gap dynamics are the main drivers of regeneration dynamics in TDF, affecting forest composition and structure (Quigley and Platt, 2003). Seasonality as an integral aspect of TDF is well known to affect phenological processes that control vegetative growth and plant reproduction, thereby controlling the regeneration of these forests (Frankie et al., 1974; Opler et al., 1980). However, the importance of gap dynamics has been suggested for tropical rainforests but remain to be tested in TDF where light dynamics and water availability change annually and tree mortality usually occurs with dead standing stems. Therefore, the main mechanisms of succession and regeneration of TDF still remain unexplored and more efforts are required to understand ecological processes of these important ecosystems.

The main goal of this synthesis for this special issue on the ecology and management of TDF in the Americas is to present a summarized review of the current knowledge of the ecology and management implications associated to TDF succession. We explore specific issues associated to ecological succession with emphasis on the use of chronosequences, plant diversity and composition, plant phenology and remote sensing, pollination, and animal–plant interactions, all under the integrating umbrella of ecosystem succession. We also emphasize the need to conduct socio-ecological research to understand changes in land-use history and its effects on succession and forest regeneration of TDF. We close this paper with some thoughts and ideas associated with the strong need for an integrating dimension not considered until today: the role of cyberinfrastructure and eco-informatics as a tool to support sound conservation, management and understanding of TDF in the Americas.

2. Ecological succession

2.1. The role of chronosequence work applied to TDF

In general, different approaches have been proposed to study succession: long-term study, stratigraphy, palynology, stand reconstruction and chronosequences (Johnson and Miyanishi, 2008). Among these approaches the chronosequence has been one of the most used methods (Chazdon et al., 2007). This method uses multiple sites of different ages to examine successional changes of plant species composition in communities (Lehmkuhl et al., 2003; Kalacska et al., 2005). Chronosequence studies have provided extensive information on successional patterns of tropical forests in a variety of life-zones, soil types, and land-use categories (Aplet and Vitousek, 1994; Zimmerman et al., 1995; Aide et al., 2000; Pascarella et al., 2000; Rivera et al., 2000; Kennard, 2002; Kalacska et al., 2005; Madeira et al., 2009). These studies have emphasized the importance of age since abandonment and land-use history on forest structure and species composition (Aide et al., 1996; Pascarella et al., 2000; González-Iturbe et al., 2002; Kalacska et al., 2005; Madeira et al., 2009). However, strong criticism has been formulated about the use of chronosequences. This criticism is centered on the fact that the main assumption associated to chronosequence research, that each site on a given chronosequence has the same history of both abiotic and biotic components, is difficult to prove. This former assumption is almost impossible to achieve, particularly in the tropics where there is a high degree of spatial heterogeneity. Indeed, most chronosequence studies justify their use by considering sites with similar soil type, topographic position and/or land-use history (Pascarella et al., 2004; Bischoff et al., 2005; van Breugel et al., 2007; Lebrija-Trejos et al., 2008; Vargas et al., 2008).

Some long-term studies, concerned about the limitations on approaches applying chronosequences have been conducted to determine whether changes that actually occur over time within sites do in fact represent different successional stages (Sheil et al., 2000; Sheil, 2001; Pascarella et al., 2004; Chazdon et al., 2007). Trends in attributes such as basal area have been adequately predicted from chronosequences (Chazdon et al., 2007; Pascarella et al., 2004) whereas differences are found with respect to species richness/density (Sheil, 2001; Pascarella et al., 2004; Chazdon et al., 2007) and species composition (Chazdon et al., 2007; Johnson and Miyanishi, 2008).

As an alternative to chronosequences, the tracking of permanent plots has been proposed as an approach complementing space–time substitution with direct observations (Swaine et al., 1987; Finegan, 1996; van Breugel et al., 2007; Chazdon et al., 2007). Although this method is considered ideal, temporal monitoring requires a significant amount of human and financial resources that usually limits the number of sites that can be tracked across time. In addition, because of the high environmental heterogeneity and beta diversity inherent to the tropics, especially in TDF (Duivenvoorden, 1995; Givnish, 1999; Balvanera et al., 2002), patterns inferred solely from a small number of permanent plots cannot be used for predicting patterns of successional change in other regions or even in other areas within the same region. In fact, the great number of factors influencing the successional process in the tropics (Guariguata and Ostertag, 2001) precludes modeling from a small number of permanent plots.

In the context of the information provided above, the use of permanent plots must be reconsidered given the restrictions imposed. Chronosequences provide a better approach to overcome these restrictions. The advantages of this methodology allow sampling of several replicates of each stage that represent the heterogeneity of plant communities and describe the community dynamics in the short term while tracking sites through time. Given the high rates of deforestation present in TDF and the subsequent urgency to generate proper management strategies, it is necessary to develop models of regeneration using a unified methodology and the chronosequence approach seems to be the most feasible.

2.2. Functional groups and succession

Another important issue in the study of succession in the context of forest management is related to function of species at each successional stage. Functional studies in the context of succession are almost absent from the TDF literature (Alvarez-Añorve et al., 2008). In the wet tropics the general trend over the last 40-years has been towards focusing on which group of species dominate a given successional stage, provoking in turn a deficit in our understanding of the fundamental aspects of functional groups (Finegan, 1996; Foster et al., 1999). Further, there has been little integration of the structural and functional characteristics and processes that occur during tropical secondary succession (Guariguata and Ostertag, 2001).

Today, most of the available succession models provide reasonable predictions of species composition but they have the main limitation of coming from temperate zones where biodiversity, and thus ecological redundancy, is lower (Dobzhansky, 1950; Naeem et al., 1994; Peterson et al., 1998; Gaston, 2000). Tropical ecosystems are the most diverse systems on the earth and this implies the highest levels of ecological redundancy as well (Ewel et al., 1991; Peterson et al., 1998). Given this fact, it is unrealistic to make specific predictions about the role of a particular species in tropical forest communities in a system where a multiplicity of species can fit in a given niche. We believe that successional approaches for the tropics should therefore substitute identity for functionality by means of considering functional units (i.e., functional groups where many plant species can perform similar functions) instead of species in their assumptions. Taking into consideration the role that ecosystem function plays in the provision of environmental services (social and economic development) (Sanchez-Azofeifa et al., 2005), our proposed approach, could help define when a given ecosystem function returns to pre-disturbance levels from a functional perspective (Guariguata and Ostertag, 2001).

Future successional studies in the tropics should take into account different ecological and site-related variables in order to determine: (1) autogenic and allogenic factors (acting on the spatial-temporal scale) influencing attributes of communities during succession; (2) functional groups dominating the different successional stages which will allow the development of models based on functional groups instead of species; (3) rate of change of the communities (in terms of their structural and functional attributes) which will allow us to understand community dynamics. In conclusion, we propose a functional approach incorporating the natural variation inherent to tropical systems as the level of analysis for the succession in TDF. This implies the proper use of chronosequences and, when possible, their tracking over time.

2.3. Plant diversity, and structure under succession

In general, studies on tropical dry forest plant communities, mainly based on a chronosequence approach under different successional stages, have found a progressive increase in tree species richness and diversity from early to late stages (e.g. Roth, 1999; Weaver, 2000; Kennard, 2002; González-Iturbe et al., 2002; Saha, 2003; de Souza and Batista, 2004; Kupfer et al., 2004; Ruiz et al., 2005; Kalacska et al., 2005; Kinhal and Parthasarathy, 2008; Lebrija-Trejos et al., 2008; Madeira et al., 2009; Quesada et al., in press). However when considering shrubs and lianas, an opposite trend is found (e.g. Weaver, 2000; González-Iturbe et al., 2002; Kinhal and Parthasarathy, 2008; but see Kupfer et al., 2004; Madeira et al., 2009).

Vegetation structure follows the same pattern of tree species richness (Kennard, 2002; Read and Lawrence, 2003; Saha, 2003; de Souza and Batista, 2004; Kupfer et al., 2004; Ruiz et al., 2005). Nevertheless, some plant attributes differ in the rate of recovery (Read and Lawrence, 2003; Ruiz et al., 2005; Lebrija-Trejos et al., 2008). For example, while canopy cover reached 75% of mature forest values in eight years, it took 23-years for basal area to reach this level (Kennard, 2002). In terms of species composition, sites in early successional stages tend to differ considerably from sites in late successional stages (Weaver, 2000; González-Iturbe et al., 2002; Kupfer et al., 2004; Madeira et al., 2009, but see Velazquez and Gomez-Sal, 2007).

Although land-use change is projected to have the largest global impact on biodiversity by the year 2100 (Sala et al., 2000), a large gap still exists in the knowledge of plant attributes during succession. Future investigations on succession should focus on: (1) changes in diversity, composition, and structure of non-woody species during succession, since most of the studies ($\sim$73%) focus on woody species, even when approximately 55% of plant species in TDF are non-woody species (Quesada et al., in press); (2) gaining specific knowledge of plant life history traits (e.g. sexual, asexual reproduction and resprouting capacity) in order to elucidate how plant functional groups respond under different types, frequency and magnitude of disturbances; and (3) how rates of change of forest structure and composition change as a function of distance from mature forests (since this should affect the establishment of propagules).

2.4. Plant phenology and remote sensing under succession

Over the ecological succession, the process of species replacement changes forest diversity and composition, and most certainly the phenological dynamics of the community. One of the first studies to address plant reproduction, phenology and ecological succession within the tropics was by Opler et al. (1980). However, there is still a lack of studies that analyze the changes on phenology across the different stages of tropical forest succession (but see Kalacska et al., 2005).

Tropical dry forests present a very seasonal phenology shaped by a long and severe dry season. Growth and reproduction are limited mostly by a short wet season that also limits the possibilities of seed germination, seedling establishment, regeneration and the process of natural dry forest succession (Opler et al., 1976). Baruah and Ramakrishnan (1989) indicate changes on leafing phenology over dry forest successional stages. Kalacska et al. (2005) also found evidence for seasonal variation in Leaf Area Index (LAI) for three successional stages in a tropical dry forest pointing out differences in timing of leaf fall according to successional stage and functional group (i.e., lianas and trees).

Among the few outcomes from the limited phenology–succession research, Kang and Bawa (2003) found little evidence for changes on flowering time with successional status, although flowering was longer in the early successional species than in late successional species, and supra-annual flowering was less common in early successional species compared to late ones.

Phenological studies of TDF also play a key role on remote sensing studies since they represent a key element to understand large scale monitoring efforts aimed to document local, regional and global ecosystem processes (e.g. Net Primary Productivity). Models aimed to link forest productivity across chronosequences using remote sensing need ground level information to better understand the temporal and spatial variability of key variables such as Photosynthetically Active Radiation (fPAR) and Leaf Area Index (Sanchez-Azofeifa et al., 2005). fPAR and LAI remotely sensed derived information can be used in combination with spectral vegetation indexes (such as the Normalized Difference Vegetation Index, NDVI) to develop light use efficiency models (LUE). LUE information can, in turn, be used to understand the role that *potential* photosynthesis plays in ecosystem function.

Presumably, seasonal phenology, including timing of leaf emergence and leaf drop, should be clearly definable by Absorbed Photosynthetically Active Radiation (APAR) using remote sensing algorithms. These remote sensing derived information can help explore more challenging ecological questions such as whether there is significant seasonal or daily variation in light use efficiency within TDF, and how species-level variation affects the overall stand productivity. The answer to this question for TDF is limited by the current lack of hypertemporal observations of NDVI and fPAR as presented by Jenkins et al. (2007) and Wilson and Meyer (2007). Previous work (e.g. Gamon et al., 2005) suggests that TDF exhibit considerable variability in both the APAR and efficiency terms of this model, indicating a variety of functional responses to physical stresses. Consequently, efforts should be made to detect functional diversity (physiological, biochemical, genetic and taxonomic diversity) with remote sensing observation through algorithms applied to TDF. Of particular interest are the role of specific photosynthetic pathways (e.g. CAM vs. C3 or C4 plants) and inverse phenology (plants maintaining green canopies in the dry season). With the increasing availability of hyperspectral sensors (instruments that measure light reflectance in the 100s of bands in contrast with sensors such as Landsat Thematic Mapper (e.g. ETM+) that measures reflectance using only seven spectral bands), our ability to address these functional questions with remote sensing will improve in the years to come. In addition, new monitoring efforts based on wireless sensing networks, that allow for an exponential increase in concurrent measurements of environmental variables, such as PAR, in combination with advanced geo-statistical approaches are providing significant paradigm shifts in understanding how light is being absorbed by the TDF canopies.

TDF research priorities should include analyses of duration of deciduousness, timing of vegetative bud break, leaf longevity, water relations, seasonal flowering types and asynchrony for different functional groups (Singh and Kushwaha, 2005), as well as a strong linkage to remote sensing studies ranging from leaf level to landscape level. The future research on ecological succession in TDF must combine floristic and structural information of early successional stages and its phenological dynamics with a strong linkage to remote sensing observations. The differential response of species to environmental cues over succession status may be a cue for our understanding of TDF succession and the observation of correct action for its conservation.

2.5. Pollination in relation to ecological succession

The tropics are particularly diverse in pollination systems (e.g. Ollerton et al., 2006) and animal pollination is by far the main pollination mode (e.g. Bawa, 1990; Chazdon et al., 2003; Quesada et al., in press). In addition, the large proportion of plant species in TDF that potentially need pollen vectors for their reproduction (5–18% monoecious, 3–23% dioecious and 54–80% self-incompatible; Machado and Lopes, 2004 and references therein; Quesada et al., in press) highlights the importance of this mutualism. Given that pollination limitation is more marked in species-rich regions (Vamosi et al., 2006), it is not surprising that disturbance is particularly strong for tropical species (Quesada et al., in press). The susceptibility of this mutualism to habitat disturbance is clear, but how different taxa re-colonize disturbed habitats and/or recover, and how these interactions are re-established is much less understood (e.g. Becker et al., 1991; Aizen and Feinsinger, 1994; Quesada et al., 2004; Cane et al., 2006; Brosi et al., 2008).

Pollination in relation to ecological succession remains highly unexplored. The literature has addressed changes in animal communities that include pollinators, mainly bats (Willig et al., 2007; Barlow et al., 2007; Avila-Cabadilla et al., 2009), bees (Fussell and Corbet, 1992; Gathmann et al., 1994; Steffan-Dewenter and Tscharntke, 2001; Vulliamy et al., 2006; Krauss et al., 2009; Moretti et al., 2009) and butterflies (Steffan-Dewenter and Tscharntke, 1997; Benes et al., 2003; Barlow et al., 2007). Possibly due to the different systems and time scales used, no consistent patterns in species richness or abundance emerge within a pollinator group on these studies. Nevertheless, there are marked differences in species composition and structure among successional stages (Steffan-Dewenter and Tscharntke, 2001; Barlow et al., 2007; Moretti et al., 2009; Avila-Cabadilla et al., 2009). Notably, different taxa respond in a more similar way when community structure is analyzed (Barlow et al., 2007). But even when identifying the responses of a particular pollinator group, it is difficult to predict the impacts on plant reproductive success, as these can be species-specific (e.g. Quesada et al., 2004).

Studies on plant communities have taken place mainly in the tropics (but see Prach et al., 1997; Prach and Pysek, 1999; Abe and Kamo, 2003), and focus on comparing pioneer and persistent species (Ibarra Manriquez and Oyama, 1992; Rosales et al., 1997; Davies and Ashton, 1999), analyzing plant communities in second-growth forests (Loiselle and Blake, 1994; Jaimes and Ramirez, 1999) or along successional gradients (Opler et al., 1980; Chazdon et al., 2003; Quesada et al., in press) in terms of their sexual and mating systems, and their pollination syndromes. It seems that species can be pioneers regardless of their sexual system (see Ibarra Manriquez and Oyama, 1992; Rosales et al., 1997; Davies and Ashton, 1999), nevertheless, the two studies that look at TDF, show that dioecy is absent in grasslands (Quesada et al., in press); and its proportion increases towards mature forests (Opler et al., 1980; Quesada et al., in press). This pattern agrees with the fact that trees hold the greatest proportion of dioecious species (Quesada et al., in press), and tree diversity increases with successional age. While these studies do reflect the importance of animal pollination throughout succession, they do not consistently assess whether putative pollinators are present in secondary forests, which precludes comparisons of the flower visitors of the same plant species across the successional gradient.

A few noteworthy studies have looked at plant–pollinator interactions along succession. Parrish and Bazzaz (1979) focused on differences in plant species niche breadth and niche overlap in pollinator use, but also in pollinator community composition and plant mating systems, in Illinois, USA (Parrish and Bazzaz, 1979). Ramirez (2004) looked at differences in pollination mode frequency along succession in a tropical dry forest of the Venezuelan Central Plain. Interestingly, Ramirez (2004) and Opler et al. (1980) coincide in concluding that bee pollination is the most common pollination mode along succession, although the proportion of each pollination mode changes among successional stages. Similarly, Chazdon et al. (2003) found insect pollination to be the most common mode, with variations in proportions of pollination modes along the succesional gradient of a rain forest in Costa Rica. Ramirez (2004) also found that pollination modes were significantly associated and affected by life forms, which are in turn associated with successional status.

Future work should focus on community level plant–pollinator interactions occurring during succession. Apart from the expected direct impacts of habitat disturbance on these interactions, there are indirect ways in which they can be affected. The inherent strong seasonality of TDF suggests that changes in flowering phenology at the species and community levels in secondary forests might have strong effects on pollinator populations, pollinator foraging patterns, plant-pollinator interactions, and plant reproduction. TDF hold many pollinator species that depend on sequential flowering in these systems (e.g. Lobo et al., 2003; Stoner et al., 2003) and changes in synchrony, for example, can affect genetic relatedness of plant populations (Fuchs et al., 2003), reproductive output and mating patterns of plants (Quesada et al., 2004). Changes in mating systems have been associated to disturbance (Quesada et al., 2001; Fuchs et al., 2003; Aguilar et al., 2008), and given the high incidence of self-incompatibility in TDF, plants might respond to a shortage of pollinators with changes in their mating systems, with consequences on gene flow and the genetic diversity.

A key approach to gain understanding of responses of plant–pollinator communities to succession can be the use of pollination networks (e.g. Memmott, 1999; Bascompte et al., 2003; Lopezaraiza-Mikel et al., 2007), which retain the detail of plant–pollinator interactions at the specific level, while working at the community level. Currently, no pollination network study has studied succession (but see Pauw, 2007; Forup et al., 2008). Several lines of future research will be important for better understanding pollinators in the context of TDF succession including: (1) analysis of pollinator assemblages and pollination web structure along successional gradients; (2) the analysis of generalization patterns of plants, animals and networks in response to succession; (3) exploring functional diversity vs. species diversity in succession (i.e. if there is species redundancy and therefore functional stability. See Fontaine et al., 2006; Moretti et al., 2009); and (4) testing predictions regarding network responses to habitat alterations (Memmott et al., 2004; Fortuna and Bascompte, 2006) and susceptibility of specialized species given pollination networks structure (Bascompte et al., 2003; Ashworth et al., 2004; Bascompte et al., 2006; but see Blüthgen et al., 2008). Furthermore, network studies on succession promise to shed light on processes of community assembly, providing empirical evidence from complex communities.

Finally, landscape level studies considering succession will unmask the relevant spatial scales and the characteristics of the landscape matrix at which different pollinator groups respond, with important contributions for conservation and landscape management. Native pollinators contribute to provisioning environmental services by actively being involved in the process of fruit and seed production in plants used by humans; and in plants involved in the regeneration and maintenance of natural forests (Ashworth et al., 2009). Understanding the role of pollinators in ecological succession is key for the management and conservation of natural forests and nearby croplands.

2.6. *Seed dispersal in relation to ecological succession*

Seed dispersal is an integral part of successional and regenerative processes in tropical ecosystems (Hardwick et al., 2004). A recent review using more than 500 studies shows that, on average, in TDF approximately 30% of seed dispersal occurs by anemochory, 27% by autochory and 43% by zoochory (Quesada et al., in press). In tropical dry forest regions, succession often begins in abandoned pastures or agricultural fields that are allowed to go fallow (Uhl, 1987; Uhl et al., 1988). Early successional areas lacking nuclear trees most frequently are colonized by wind-dispersed species (Janzen, 1988). Successful colonization by particular species within early successional areas depends not only on many microclimatic factors (Maluf de Souza and Ferreria Batista, 2004; Holl, 1999), but also on species' ability to disperse. As shown for boreal forests, several wind-dispersed species in TDF show specialized adaptations that allow predictions to be made about dispersal distances and directions (Greene et al., 2008, 1999).

Once some vegetation or nuclear trees are established within areas of early succession or abandoned pastures, these sites may be used by animals as resting or feeding areas (i.e., when they carry a fruit to consume). Although several studies have suggested that endozoochorous seed dispersal is lower in tropical dry than tropical humid or wet forests (Bullock, 1995; Jordano, 2001), some estimates in tropical dry forest are as high as 64% (Janzen, 1988; see review by Quesada et al., in press). Vertebrates are important seed dispersers in tropical forests (Howe and Smallwood, 1982); and mammals and birds, in particular, play key roles in primary seed dispersal (Stoner et al., 2007). Given this fact, changes in frugivorous animal communities during succession undoubtedly affect seeds arriving to areas undergoing succession and ultimately the emerging successional forest.

The process of succession in TDF often occurs in disturbed areas with a fragmented matrix, and forest remnants of variable sizes (Kassi et al., 2008). Under this context, the way in which fragmentation and disturbance affect particular frugivore groups will have an impact on seed dispersal to areas undergoing succession. Several studies on different vertebrate frugivore groups have shown a negative impact of forest fragmentation and disturbance on frugivore diversity and abundance (Fenton et al., 1992; Chiarello, 1999, 2003; Gorresen and Willig, 2004; Harcourt and Doherty, 2005); nevertheless, only a few studies have evaluated assemblages of frugivores in the context of successional stages (Pons and Wendenburg, 2005; Avila-Cabadilla et al., 2009). Furthermore, a direct link between changes in frugivore communities to changes in dispersed seeds or seedling establishment in successional tropical dry forest has not been shown.

The importance of nuclear trees in stimulating animal seed dispersal and facilitating the natural process of succession and regeneration was first suggested by Janzen (1988) and, more recently, several studies have supported this hypothesis. Unfortunately, most of the studies in tropical regions that have evaluated seed dispersal under remnant trees have concentrated their efforts in tropical humid or wet forests (Toh et al., 1999; Zahawi and Augspurger, 1999, 2006; Shiels and Walker, 2003; Guevara et al., 2004; Schlawin and Zahawi, 2008; but see Hardwick et al., 2004). Directed dispersal may be important for ecosystem management and restoration programs (see Hardwick et al., 2004 for a review). In particular, accelerating natural regeneration by erecting perches to encourage seed dispersal by bats and birds is one of the most promising active management programs (McClanahan and Wolfe, 1993; Holl, 1998; Scott et al., 2000; Wenny, 2001; Kelm et al., 2008). Nevertheless, most of these so far have been tested in tropical humid or wet forests and research is generally lacking in TDF.

In conclusion, there are several aspects of seed dispersal in successional areas of tropical dry forest that require further investigation. First, a modeling approach for wind-dispersed seeds, similar to what has been used for boreal forests (Greene et al., 1999), would be useful in helping to predict the early stages of succession. This information may help in recognizing when active management via the introduction of nuclear trees is necessary to avoid monotypic stands. Second, more information is needed on how changes in frugivore assemblages in fragmented and disturbed habitats directly influence the arrival of zoochoric seeds to successional areas. Future studies need to go beyond documenting changes in frugivore assemblages and concentrate on evaluating how these changes directly affect seed dispersal and recruitment. Third, the potential success of artificial perches for stimulating seed dispersal in areas of early succession in TDF should be evaluated. Finally, more research on germination and seedling growth in tropical dry forest species is needed to develop effective restoration programs.

2.7. Plant herbivore interactions and succession

Studies on plant–herbivore interactions and terrestrial succession have increased substantially since the last decades of the past century (see revisions in Davidson, 1993; Olff and Ritchie, 1998; Maron and Crone, 2006; Skarpe and Hester, 2007). The information on the patterns of herbivory among the various taxa during succession has been strongly concentrated in temperate regions (Davidson, 1993; Skarpe and Hester, 2007). In the tropics, in general, these studies are scarce (Brown and Ewel, 1987; Leps et al., 2001; Poorter et al., 2004). Most studies have focused on the effects of different types of herbivores on the plant community dynamics (Brown, 1985; Crawley, 1989; Davidson, 1993; Leps et al., 2001; Skarpe and Hester, 2007; Howe, 2008; Feng et al., 2009). Usually, large mammals are thought to have a stronger effect on ecosystem regeneration patterns than herbivore insects (Crawley, 1989; Olff and Ritchie, 1998; Gomez and Zamora, 2000). Nevertheless, there is considerable evidence that insects can selectively eat dominant plant species and change their colonization and/or competitive ability, either hastening or halting the successional process (Brown, 1985; Davidson, 1993; Carson and Root, 1999; Fagan and Bishop, 2000; Schädler et al., 2003, 2004; Fagan et al., 2004).

Successional changes, however, in insect herbivore communities have not received the same attention (Brown and Hyman, 1986; Hendrix et al., 1988; Brown and Gange, 1992; Edwards-Jones and Brown, 1993; Siemann et al., 1999), especially in tropical regions (but see Leps et al., 2001; Fernandes et al., in press). In Neotropical forests, large grazers and browsers are not abundant and the bulk of plant leaf biomass is in the canopy, where most of the damage is inflicted by insects (Coley and Barone, 1996). Yet these organisms may represent key elements in many processes that shape and maintain the ecosystem structure and function (Schowalter, 1981; Price, 1997). A large gap exists in the knowledge about changes in community composition, diversity patterns and the relative roles of bottom-up and top-down forces in controlling insect herbivore populations during succession. In TDF, plant–herbivore interactions are likely to be different from moist forests, since most plants drop their leaves during the dry season, leaving a substantial proportion of herbivores (folivores, leaf-miners, gall inducers) without food for six to eight months per year. The majority of the studies on herbivores conducted so far in TDF addressed seasonal changes in leaf chemistry and damage rates and insect abundance (Janzen, 1981; Janzen and Waterman, 1984; Dirzo and Domínguez, 1995; Filip et al., 1995; Boege, 2004, 2005). However, key information on how herbivores affect plants during succession and vice-versa are lacking in spite of their role in providing food for many vertebrates, and in nutrient cycling at the ecosystem level.

Future investigations on plant–herbivore interactions in TDF should focus on many avenues that include (1) herbivore effects on plant survival, growth and reproduction and how these affect species competitive ability and substitution over time in this seasonal forests; (2) bottom-up effects of forest succession on herbivore communities. In this case, it is important to determine the effects of changes in habitat structural complexity (plant richness, density and height), plant architecture and plant nutritional quality (content of water, nutrients and secondary compounds) on herbivore diversity and consumption rates; and (3) top-down regulation of herbivore populations, since the abundance of natural enemies, such as parasitoids, spiders and vertebrates, is likely to change with habitat complexity during succession.

Bottom-up interactions through density-dependent plant–herbivore interactions are likely to regulate plant populations under succession. Therefore, management of herbivore populations will determine the structure and composition of plant communities through succession. For example, disappearance of natural enemies from the community may cause an outbreak of certain plant species and over-dominance in the community. On the other hand, it is also possible that herbivores can be used to control populations of invasive plant species to facilitate the establishment of natural populations that could have been displaced. Management and regeneration programs should consider the experimental manipulation of herbivores.

3. Social and management aspects of succession

Understanding TDF transformation by human activities requires not only the analysis of impacts on ecosystem composition, structure and functioning but also an analysis of the social processes that drive human decision making and the way that human perceptions of their environment affect forest management decisions. Apart from analyzing how TDF provide ecosystem services to human societies, profound analysis of the economic, political and cultural aspects that explain land-use and land-use changes are extremely needed in the Americas where in general, as discussed above, are heavy biases towards wet forests.

TDF conversion for cattle has been identified as one major cause of its fragmentation and degradation in the Americas (Trejo and Dirzo, 2000; Quesada and Stoner, 2004; Miles et al., 2006; Calvo-Alvarado et al., 2009; Espírito-Santo et al., 2009). This land cover change process has been generally driven by governmental policies based on the perception that TDF were “useless” and should be cleared for intensive agricultural production (Sanchez-Azofeifa et al., 2001; Castillo et al., 2005; Calvo-Alvarado et al., 2009). Although TDF provides societies with many wood and non-wood products (Quesada and Stoner, 2004), economic pressures explain cases of over-extraction of resources, as for example fuelwoods for charcoal production in Brazil (Ratter et al., 1997).

Studies that document small farmer’s view points on TDF use, conservation and restoration, recognize that TDF provides ecosystem services such as fuel wood, forest fruits, medicinal plants, timber or animals for hunting, but human induced restoration is not perceived as important or necessary (Cordero, 2005). Re-sprouting capacity of TDF species is identified also by some small farmers as a natural mechanism that will impede TDF disappearance and that will allow them to continue extracting wood for family and local use (Schroeder, 2006). However, such management practices need more empirical evidence. Elmqvist et al. (2007), also argue that TDF regeneration can be influenced by management practices developed by local institutions (i.e., norms and rules for TDF use which are based on secure property rights). Consequently long-term maintenance and delivery of ecosystem services of TDF depend upon complex socio-ecological resilience.

Another issue related to human activities that deserves a better understanding is the transformation of tropical forests through current forest management practices that claim the sustainable exploitation of timber trees from natural forests (Sheil and Van Heist, 2000). The idea is that forest logging and silvicultural practices are extrinsic forest disturbances designed to create patterns similar in size and intensity to apparently intrinsic natural disturbances such as tree falls (e.g. Skorupa and Kasenenek, 1984). Such management practices propose that natural regeneration and gap forest dynamics can be applied to the sustainable management of tropical forests (e.g. Brokaw, 1987; Denslow, 1987; Brandani et al., 1988). Unlike the harvesting systems commonly employed in temperate regions, harvesting in tropical forests usually employs selective polycyclic systems, where only a proportion of stems, usually the largest, are cut. Then the same harvested or treated compartment will be revisited after the younger trees have apparently grown sufficiently (see Hartshorn, 1978; Clark, 1994, 1990; Whitmorte and Brown, 1996; Brown and Jennings, 1998).

Despite their claim of sustainability, such forest management practices supposedly allow the sustainable extraction of timber from natural forests by local human communities. However, such practices have severe limitations that need to be addressed to prevent destruction of tropical forests that in the long term will negatively affect local human communities that depend on forest timber (Uhl et al., 1988; Sheil and Van Heist, 2000; Costa and Magnusson, 2003; Lobo et al., 2007). Some of the main ecological issues that question these forest management practices and require serious scientific analysis are: (1) tree falls occur because of dead, hollow or vulnerable trees and hence forest harvesting would imply an increase in forest disturbance (Uhl and Guimarães-Vieira, 1989; Barrantes et al., 1999; Putz et al., 2008); (2) harvested forest gaps are generally larger than natural gaps which more likely favor the regeneration of pioneer and sometimes exotic invasive species, simplifying and homogenizing the forest diversity and structure (Barrantes et al., 1999; Costa and Magnusson, 2003; Putz et al., 2008); (3) removal of larger stems will negatively affect subsequent regeneration due to loss of fruit and seed sources (Barrantes et al., 1999; Costa et al., 2002; Lobo et al., 2007); (4) forest management will negatively affect the role of many animal species in pollination and seed dispersal that is often species-specific and difficult to replace; and (5) knowledge of the reproductive attributes of timber tree species is surprisingly limited (Barrantes et al., 1999; Quesada and Stoner, 2004). Hence tropical dry forest ecological research directed to generate additional information along these lines will be important to help resolve many technical uncertainties in order to improve sustainable forest management and habitat maintenance.

4. Eco-informatics and cyberinfrastructure to unify remote sensing, ecological monitoring and socioecosystem data

With the emergence of faster micro-processors and advances on database development in the ecological and environmental fields, eco-informatics is becoming a critical element for data integration and modeling. Eco-information is defined as a set of tools and metadata standards that help the scientific community to define complex patterns in ecological and environmental data. Eco-informatics is complemented via the implementation of cyberinfrastructures. Cyberinfrastructure is defined as the development of new research environments that support advanced data acquisition, data storage, data management, data integration, data mining, data visualization and other computing and information processing services over the Internet (Atkins et al., 2003). Applications of cyberinfrastructure and eco-informatics tools to TDF is in its infancy, and significant challenges remain in integrating remote sensing ecological information with social data. In general, informatics tools for remote sensing are relatively well-developed, but do not link well to ecological data, although efforts are underway to develop these tools (Gamon et al., 2006).

A particular challenge lies in the paucity of databases and metadata for ecological data, and the diversity of data formats associated with ecological studies. Social data, particularly qualitative studies (case studies) do not lend themselves to rigid database structures, and are restricted by the limitations placed on human subjects by ethic restrictions regarding data accessibility and distribution.

Despite these limitations, integrated and inter-disciplinary studies such as those funded by the Inter-American Institute for Global Change Research (IAI) under its Collaborative Research Network program (e.g. Tropi-Dry) offers a powerful platform for exploring the potential of integrating remote sensing, ecological and social science data. The unified methodology across countries and sites, along with specific spatial location, allows a degree of project integration that would not otherwise be possible. For ecological and remote sensing variables that can be linked in time and space (via time and date stamps, GPS coordinates), the emerging Tropi-Dry databases offer potential for project integration that is facilitating a functional understanding of evolving forest dynamics. Here, it is key the multi-scale sampling design that explicitly links field sampling to automated optical sampling and remote sensing. For example, seasonal patterns of LAI and fPAR data (collected on the ground) can be readily linked to the time-stamped data from stations designed to record daily phenological changes of the plant community, and GPS coordinates will allow explicit linkages to remotely sensed imagery. These efforts, linking field data with remotely sensed imagery, are proving critical to proper validation of satellite data, enabling extrapolation of these studies to larger regions.

For social science data that often lack explicit space–time coordinates, a potential linkage is through political boundaries that can be linked in space and time to ecological field data and remote sensing. For example, the contrasting land-use histories across countries are clearly captured both in the social science analyses and in the satellite imagery, allowing for more powerful analyses than would be possible from any single source.

5. Final conclusion

Overall, a major effort to describe general patterns of succession of TDF, the management practices that create them and their ecological significance must be made. In addition, a significant move from specific predictions that can be extremely site-dependent, to large landscape level estimations using emerging remote sensing techniques is necessary. Description of patterns across different latitudes, for example, would generate a powerful model applicable to the whole system in the long term. Information inferred from these kinds of models would be extremely useful for the current knowledge, management and conservation of this important ecosystem as well as for understanding their responses to disturbance (natural or anthropogenic) and climatic change at the continental level.

Further additional suggestions to enhance our understanding of linkages between ecology and management of TDF are:

(1) Tropical secondary succession must no longer be considered as a simple, unidirectional and linear sequence of change in

functional groups/species composition. New approaches, such as state and transition models, can be explored in order to explain the high variation found in a single successional stage as well as the persistence of some states in the tropics.

(2) We propose successional models based on functional groups more than species composition models. These models could be more reliable to predict the structural and functional attributes of the communities under succession, making the sequence of processes predictable even if the species composition is not completely known. For example, assemblages of ecophysiological, morphological and spectral plant traits should be of great utility to characterize tropical functional groups. Some of these traits can now be detected and analyzed with modern techniques of remote sensing, allowing for large scale studies of vegetation at a landscape level. This would constitute a powerful tool for the study of forest dynamics.

(3) Well-designed chronosequence studies with replicated site ages, quantitative and qualitative measurements of environmental variables, and appropriate multivariate analyses are an important tool for examining long-term successional patterns (Pascarella et al., 2004).

(4) We propose the study of pollination networks to gain understanding of responses of plant–pollinator communities to succession. Further research will allow for analysis of pollinator assemblages and pollination web structure along successional gradients and for exploring functional diversity in relation to species diversity in succession for testing predictions regarding network responses to habitat alterations. Landscape-level studies considering succession will help understand the role of pollinators in conservation and landscape management.

(5) Future investigations on plant–herbivore interactions should focus on analyzing bottom-up or top-down effects of forest succession on herbivore communities. Management of herbivore populations through these trophic relations determines the structure and composition of plant communities by regulating populations under succession.

(6) There are several aspects of seed dispersal in successional areas of tropical dry forest that require further investigation. First, a modeling approach for wind-dispersed seeds, similar to what has been used for boreal forests (Greene et al., 1999), would be useful in predicting early stages of succession. Second, more information is needed on frugivore assemblages and dispersal of zoochoric seeds in different successional stages. Third, the use of artificial perches for seed dispersal and regeneration of early succession of TDF should be evaluated. Finally, more research on germination and seedling growth in tropical dry forest species is needed to develop effective restoration programs.

(7) We should identify the main parameters involved in TDF succession to develop models of recruitment dynamics of key dry forest plant species that facilitate the process of succession following natural or human-induced disturbances.

(8) Collection of reliable basic socio-ecological information and detailed land-use histories from local peasants and its effects on forests regeneration is becoming a relevant research goal for understanding TDF succession and it has also implications when thinking about restoration needs, particularly in the context of constructing management alternatives that allow TDF conservation and sustainable use.

Finally, multidisciplinary efforts to unify information on ecological, remote sensing and human dimensions of tropical dry forest research are necessary if we really want to make a difference in achieving sound sustainable development policies. The information generated from this disciplines is crucial for decision-makers and for the management and sustainable development of TDF across the Americas.

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