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Disturbance and Resilience in Tropical American Palm Populations and Communities

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Abstract We review resilience to natural and anthropogenic disturbance of palm populations and communities in tropical America. Response of palms to disturbance depends on their morphological traits, their reproductive strategies and the impacts of these traits and strategies on phenology and gene flow. Human impact induces changes in genetic structure, increasing endogamy and genetic drift in fragmented populations. Forest fragmentation and harvest of palm organs are well documented whereas effects of intermediate disturbance like selective logging, hunting or fire remain poorly known. We recommend emphasis on long-term experiments and on the use of mechanistic approaches in future research to facilitate integration of available data into a theoretical ecological framework.

Keywords Arecaceae · Deforestation · Gene flow · Harvest · Tropical America · Pollination · Resilience · Seed dispersal

Introduction

In the context of the global, ever-increasing human impact on the Earth's biomes, it is important to understand mechanisms that regulate ecosystems, control their capacity to absorb disturbances and maintain their biodiversity. One of the most striking manifestations of global human impact is deforestation, especially in humid tropical countries (Hansen et al., 2010), where the richest—and least studied—forest ecosystems ocurr (Pitman, 2010). Globally, tropical forest cover is decreasing (Gibbs et al., 2010; Hansen et al., 2010) and most of the remaining forested areas are in a disturbed state (Mayaux et al., 2005).

Alteration and decrease in tropical forest cover is not only a concern for biodiversity conservation and biosphere stability, but also for the future and well-being of human populations, through the crucial ecosystem services that tropical

forests provide. Ecosystem services include conservation of soils, carbon uptake, regulation of water cycles and local climate, control of populations of disease vectors. Subsistence and trade services are provided by harvested products for food, construction, tools, fabrics, combustibles, medicine, etc. (Ehrlich & Ehrlich, 1992; Carpenter et al., 2006a,b).

The sustainability of ecosystem services depends on ecosystem resilience, i.e. "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" (Walker et al., 2004). Resilience is generally discussed at the ecosystem level and related to ecosystem services in a socio-economic context (e.g. Meijaard et al., 2010). Since tropical forest ecosystems are particularly complex, a relevant approach to characterize their resilience abilities is to assess the functioning of their key components individually (Schaberg et al., 2008). Forest ecosystem resilience is maintained provided that secondary succession dynamic is active, so increasing attention is being paid to this process in tropical forests (Lowe et al., 2005; Sezen et al. 2005; Babweteera & Brown, 2009; Norden et al., 2009; Letcher, 2010).

Within its resilience limit, an ecosystem is able to recover and return to its initial equilibrium after release of the disturbance driver (Holling, 1973). However, as soon as disturbance exceeds the resilience threshold, a regime shift occurs, that can alter seriously the benefits provided by the initial system (Folke et al., 2004; Lambin, 2005; Brock & Carpenter, 2006).

Palms in the tropical America are ideal candidates to examine resilience at the species level. Tropical American palms are diverse, with 459 species in 50 genera recorded in South America (Pintaud et al., 2008b), and at least 150 species in 25 genera in Central America (Henderson et al., 1995). Tropical American palms are also commonly gregarious and locally abundant (Terborgh & Andresen, 1998; Arroyo-Rodriguez et al., 2007), forming up to 72% of the canopy cover locally (Kahn & de Granville, 1992). This is particularly noteworthy in tropical forests where the high tree diversity generally results in a low density of each treelike species (Lieberman & Lieberman, 2007). The keystone properties of palm populations make them essential components of tropical forests, influencing deeply the structure and the functioning of these ecosystems. Their importance can be described in terms of biomass, vegetative cover, effect on tree recruitment and other competitive interactions with plants (Vandermeer, 1977; Wang & Augspurger, 2004; Peters et al., 2004; Aguiar & Tabarelli, 2010), role in nutrient turnover, interactions with phytophages, dispersers and pollinators (e.g. Wright & Duber, 2001; Galetti et al., 2006; Stone, 2007). From a socio-economic standpoint, tropical American palms are considered a major resource (Henderson et al., 1995) as fruits, leaves, stems, seeds, sap and other parts are exploited, destructively or not, for numerous purposes (Macía, 2004; Balslev et al. 2008; Galeano & Bernal, 2010). Human-induced disturbances that may cause the loss of such species should have dramatic consequences for the ecological functioning of tropical American ecosystems (Arroyo-Rodriguez et al., 2007) and for the crucial services these species provide.

The disturbances affecting palm resilience in tropical America are primarily related to deforestation. This may be a direct effect, through clearcutting or selective logging (Svenning, 1998), which generate microclimatic stress by changing local

temperature and relative humidity (Laurance et al., 2001). These changes may exceed the physiological limits of palms and lead to the extinction of palm populations in deforested areas. Deforestation also has indirect effects on palm populations, through habitat fragmentation, including edge effects, especially with a higher mortality of large-seeded, slow growing, old-growth trees (Scariot, 1999; D'Angelo et al., 2004; Laurance et al., 2004), and the alteration of seed dispersal through depletion of populations of seed dispersers (Wright & Duber, 2001; Chapman et al., 2010; Becker et al., 2008). Other disturbances include harvest of non-timber forest products (NTFPs) of palms, which is particularly widespread in the tropical America (e.g. Galeano & Bernal, 2010), herbivory by domesticated animals, game hunting, fire and natural disturbances (Fearnside, 2002). Disentangling the effects of each of these disturbances on the resilience of palm populations at the ecological and genetic levels would provide clues for the long-term conservation and sustainable use of tropical American forests.

Here we review the literature concerning resilience of palm populations and palm communities in tropical America. We ask specifically the following questions: Which are the factors underlying palm responses to disturbance? How does resilience vary as a response to different kinds of disturbance? Is the importance of palms in various geographic regions of tropical America well represented in existing studies ? How relevant are past and current methodological approaches to assess palm resilience following disturbance? Based on the answers to these questions we make recommendations for future ecological research on palms that will improve both the theoretical basis for our understanding of resilience and provide practical tools for biodiversity conservation.

Methods

We used quantitative and qualitative approaches to review the effects of disturbance on palm resilience in tropical America.

Studies relevant to ecological resilience of palm populations and communities facing disturbances were sufficiently numerous and similarly structured to perform a quantitative meta-analysis. We assessed papers referenced in the Web of Science (1975–present) containing one or more of the following keywords: palm, disturbance, (central or south) America, fragmentation, deforestation, hunting, fire, harvest, extraction, and/or defoliation. We excluded papers that (i) treat species' response to disturbance at community level with only brief mention of palm responses, (ii) that do not compare clearly defined and different levels of disturbance (e.g. Wang, 2008; Portela et al., 2010), or (iii) that deal with the effects of disturbances on palm resilience only in the discussion section (e.g. Rodríguez-Buriticá et al., 2005). A total of 45 papers (published in 1987–2010) meeting these critera were retained. These studies address the effects of various types of anthropogenic and natural disturbances on the structure and dynamic of palm populations and communities in tropical America. They include detailed information about 34 palm species, and in addition a number of species are briefly mentioned in community-level studies. The following information was extracted from each paper: type of disturbance (harvest, fragmentation, clearcutting, selective

logging, herbivory, hunting, fire and natural disturbance); type of study (experimental or observational); application of matrix models (yes, no); duration of the study ("snapshot" intsantaneous study, 1–2 years, 2–5 years, >5 years); ecological level of organization (population or community); microenvironmental abiotic data including microclimate, soil composition and moisture etc. (measured, not measured). A simple, semi-quantitative resilience index (high, medium, low) was estimated for each species in each study within the sample. High resilience corresponds to a positive or neutral response of palms to disturbance (e.g. *Sabal* spp.: higher level of leaf production under higher harvest intensities; Martínez-Ballesté et al., 2008). Medium resilience corresponds to a slightly negative or antagonistic response of palms to disturbance (e.g. *Ceroxylon echinulatum*: positive effect of selective logging but negative effect of clearcutting; Anthelme et al., 2011). Low resilience was identified as a clearly negative response to any disturbance, directly (e.g. *Sabal yapa*: lower fecundity and lower seedling survival after clearcutting; Pulido et al., 2007) or indirectly (e.g. *Euterpe edulis*: alteration of the size of disperser's populations due to habitat fragmentation; Fadini et al., 2009), that will affect indices of palm fitness (biomass, reproduction and/or survival). When two disturbances were studied for the same species (e.g. response of *Ceroxylon echinulatum* to selective logging and clearcutting; Anthelme et al., 2011) we provided two separate resilience indices. This information is summarized in Table 1. Data on life form, habitat and reproductive strategy were extracted from the publications taken into account in this study and from Henderson et al. (1995) and Galeano & Bernal (2010). Presence or absence of harvesting pressure on the considered species within the context of the studies was additionally reported, as well as an average resilience score for each species (including various types of disturbances and various studies when available). These data appear in Table 2.

Secondly, we provide a qualitative analysis of the factors underlying palm resilience, by compiling information on broad-scale/long-term factors influencing palm population dynamics, and on life history traits of palms from the continental tropical America (Takhtajan, 1986) including Mexico, Central and South America, as well as more general information on tropical tree functioning and humid forest ecosystems relevant to the topic.

Quantitative Assessment of Publications on Palm Resilience

With 45 peer-reviewed publications discussing the effects of disturbances on palm populations and communities in tropical America, there is sufficient empirical information available to assess quantitatively the locations, methods and descriptors used, as well as the main results and interpretations found on palm resilience in disturbed areas. This approach will permit (i) to characterize more accurately the current state of knowledge on palm resilience, and (ii) to propose relevant focuses for future research (Fig. 4).

Geographic Distribution of Studies

Studies of resilience of palm populations and communities are unevenly distributed across the forest ecosystems of tropical America (Fig. 1). Amazonia and Central

Table 1 Summary of Studies Addressing Palm Resilience

Type of disturbance	Reference	ME Data	Transition matrix	Biogeogaphical entity	Timescale	Method	Organisation level	Resilience level
Fr	1-Aguirre & Dirzo, 2008	−	−	Centr. Amer.	Snapshot	O	Population	Medium
Ha	3-Anderson & Putz, 2002	−	−	Amazonia	Snapshot	O	Population	Medium
Ha	3-Anten et al. 2003	−	−	Centr. Amer.	1–2 years	E	Population	High
SL	4-Anthelme et al., 2011	+	−	NW Andes	Snapshot	O	Population	High
D	4-Anthelme et al., 2011	+	−	NW Andes	Snapshot	O	Population	Low
Fr	5-Arroyo-Rodriguez et al., 2007	−	−	Centr. Amer.	Snapshot	O	Population	Low
Fr	6-Baez & Balslev, 2007	+	−	Choco	Snapshot	O	Community	Low
D	7-Barot et al., 2005	−	-	E. Amazonia	Snapshot	O	Population	Low
Fr	8-Benitez-Malvido & Martinez-Ramos, 2003	−	−	Amazonia	> 5 years	E	Community	Low
Ha	9-Bernal, 1998	-	+	Choco	1–2 years	O	Population	Medium
He	10-Berry et al., 2008	-	+	Centr. Amer.	1–2 years	O	Population	Medium
Fr	11-Bonjorne de Almeida & Galetti, 2007	−	−	South Cone Cerrado	< 1 year	O	Population	Medium
Fr	12-Brum et al., 2008	−	-	C. Amazonia	> 5 years	O	Population	Medium
Ha	13-Calvo-Irabien et al., 2009	−	−	Centr. Amer.	1–2 years	E	Population	Medium
Ha	14-Chazdon, 1991	−	−	Centr. Amer.	2–5 years	E	Population	High
Fr	15-Clement et al., 2009	−	−	Amazonia	Snapshot	O	Population	Low
He	16-Endress et al., 2004a	−	+	Centr. Amer.	1–2 years	E	Population	Low
Ha	16-Endress et al., 2004a	−	+	Centr. Amer.	1–2 years	E	Population	Medium
Ha	17-Endress et al., 2004b	−	+	Centr. Amer.	2–5 years	E	Population	Medium
Ha	18-Endress et al., 2006	−	+	Centr. Amer.	> 5 years	E	Population	Medium
Fr	19-Escalante et al., 2004	−	+	Centr. Amer.	2–5 years	O	Population	Medium
Ha	19-Escalante et al., 2004	−	+	Centr. Amer.	2–5 years	O	Population	High
Fr	20-Fadini et al., 2009	−	−	Atlantic Forest	< 1 year	O	Population	Low

Table 1 (continued)

Type of disturbance	Reference	ME Data	Transition matrix	Biogeogaphical entity	Timescale	Method	Organisation level	Resilience level
SL	21-Fleury & Galetti, 2004	−	−	Atlantic Forest	< 1 year	E	Community	High
Fr	21-Fleury & Galetti, 2004	−	−	Atlantic Forest	< 1 year	E	Community	Medium
Fr	22-Fleury & Galetti, 2006	−	−	Atlantic Forest	< 1 year	E	Population	Low
Ha	23-Flores & Ashton, 2000	−	−	W. Amazonia	< 1 year	E	Population	Medium
Ha	24-Freckelton et al., 2003	−	+	Atlantic Forest	2–5 years	O	Population	Low
Hu	25-Galetti et al., 2006	−	−	Atlantic Forest	< 1 year	E	Population	Low
Fr	25-Galetti et al., 2006	−	−	Atlantic Forest	< 1 year	E	Population	Low
Ha	26-Holm et al., 2008	−	+	Amazonia	1–2 years	O	Population	Medium
Ha	27-Martínez-Ballesté et al., 2008	−	−	Centr. Amer.	1–2 years	E	Population	High
Ha	28-Martínez-Ramos et al., 2009	+	−	Centr. Amer.	2–5 years	E	Population	Low
ND	28-Martínez-Ramos et al., 2009	+	−	Centr. Amer.	2–5 years	E	Population	Medium
Ha	29-Mendoza et al., 1987	−	−	Centr. Amer.	2–5 years	E	Population	Low
Ha	30-Moegenburg & Levey, 2003	−	−	Amazonia	< 1 year	E	Population	Medium
D	31-Norden et al., 2009	−	−	Centr. Amer.	> 5 years	O	Community	Low
SL	31-Norden et al., 2009	−	−	Centr. Amer.	> 5 years	O	Community	High
Ha	32-Oyama & Mendoza, 1990	−	−	Centr. Amer.	1–2 years	E	Population	High
Ha	33-Pedersen, 1996	−	−	W. Amazonia	1–2 years	O	Population	Medium
He	34-Pacheco, 2001	−	−	C. Amazonia	1–2 years	E	Community	High
ND	34-Pacheco, 2001	−	−	C. Amazonia	1–2 years	E	Community	Medium
ND	34-Pacheco, 2001	−	−	C. Amazonia	1–2 years	E	Community	Medium
D	35-Pulido & Caballero, 2006	−	−	Centr. Amer.	1–2 years	O	Population	Low
D	36-Pulido et al., 2007	−	+	Centr. Amer.	1–2 years	O	Population	Low
He	37-Sampaio & Scariot, 2010	−	+	Galery forest N. Cerrado	2–5 years	O	Population	Medium

Table 1 (continued)

Type of disturbance	Reference	ME Data	Transition matrix	Biogeogaphical entity	Timescale	Method	Organisation level	Resilience level
Ha	38-Sampaio et al., 2008	−	−	Galery forest N. Cerrado	< 1 year	E	Population	Medium
Fr	39-Scariot, 1999	−	−	C. Amazonia	Snapshot	O	Community	Medium
SL	40-Siebert, 2000	+	−	Centr. Amer.	1–2 years	E	Population	Medium
Ha	40-Siebert, 2000	+	−	Centr. Amer.	1–2 years	E	Population	High
Fr	41-Souza & Martins, 2004	−	+	Atlantic Forest	2–5 years	O	Population	Medium
Fi	41-Souza & Martins, 2004	−	+	Atlantic Forest	2–5 years	O	Population	Medium
Ha	42-Svenning & Macía, 2002	+	+	W. Amazonia	1–2 years	O	Population	Medium
SL	43-Svenning, 1998	+	−	NW Andes	Snapshot	O	Community	Medium
Fr	44-Wright & Duber, 2001	−	−	Centr. Amer.	< 1 year	O	Population	Low
Hu	44-Wright & Duber, 2001	−	−	Centr. Amer.	< 1 year	O	Population	Low
Ha	45-Zuidema et al., 2007	−	−	Amazonia	1–2 years	E	Population	High

Type of disturbance: D, deforestation (clearcutting); Fi, fire; Fr, forest fragmentation; Ha, harvest; He, herbivory; Hu, hunting; ND, natural disturbance; SL, selective logging. Microenvironmental (ME) data and use of transition matrices: (yes: +, no:−). Methodology: O, observational; E, experimental

Table 2 Data on Species Studied in the Set of Articles Used in the Quantitative Analysis

Species	References (from Table 1)	Understorey / canopy Tree	Aerial Stem	Clonal	Harvest	Resilience
Aiphanes erinacea	43*	U	+	+	−	low
Aphandra natalia	33	U	+	−	+	medium
Astrocaryum aculeatissimum	25	U	+	+	−	low
Astrocaryum mexicanum	1, 5, 29	U	+	−	−	low
Attalea butyracea	44	CT	+	−	+	low
Attalea geraensis	11	U	−	−	−	medium
Attalea humilis	41	U	−	−	−	medium
Attalea speciosa	7	CT	+	−	+	medium
Bactris gassipaes	15	CT	+	+	+	low
Ceroxylon echinulatum	4	CT	+	−	+	medium
Chamaedorea elegans	28	U	−	−	+	high
Chamaedorea linearis	43*	U	+	−	−	high
Chamaedorea pinnatrifrons	43*	U	+	−	−	high
Chamaedorea radicalis	16, 17, 18	U	−	−	+	medium
Chamaedorea tepejilote	33	U	+	−	−	high
Desmoncus orthacanthos	19, 40	U	−	+	+	high
Euterpe edulis	20, 21*, 24	CT	+	−	+	low
Euterpe oleracea	30	CT	+	+	+	medium
Geonoma congesta	14	U	+	+	+	high
Geonoma deversa	23, 45	U	+	+	+	medium
Geonoma macrostachys	41	U	−	−	+	medium
Geonoma schottiana	37	U	+	−	+	medium
Geonoma undata	43*	U	+	−	+	low
Iriartea deltoidea	2	CT	+	−	+	medium
Mauritia flexuosa	26, 38	CT	+	−	+	medium
Oenocarpus bacaba	12, 39*	CT	+	−	+	medium
Oenocarpus bataua	34*	CT	+	−	−	medium
Phytelephas seemannii	9	U	−	−	+	medium
Prestoea acuminata	43*	U	+	+	+	medium
Sabal mexicana	27*	CT	+	−	+	high
Sabal yapa	27,35, 36	CT	+	−	+	high
Socratea exorrhiza	34*	CT	+	−	−	high
Syagrus romanzoffiana	21*, 22	CT	+	−	−	low
Thrinax radiata	13	CT	+	−	+	medium

*For community-level studies, only the species otherwise studied at the population level are mentionned in this table

America, the richest regions for palms (Henderson et al., 1995, Pintaud et al., 2008b), are logically the most studied, but the Atlantic forest, with 35 palm species recorded, has also been the subject of a relatively high number of studies. The Pacific coast, while harbouring as many as 105 species, is represented in our

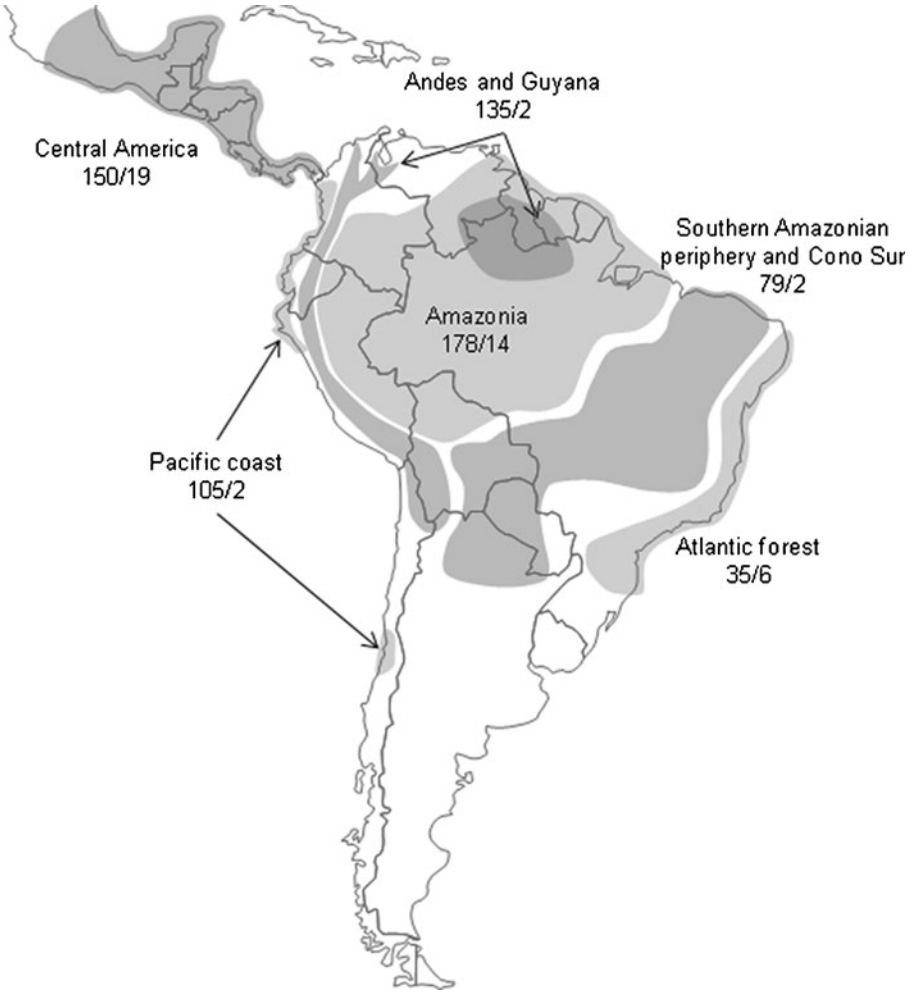

Fig. 1 Number of palm species/number of articles addressing palm resilience by phytogeographical units in the Neotropics

sample by only two studies. The Andes and the Guyana mountains (135 species) and the South Cone (79 species), are clearly understudied with respect to palm response to disturbance (two and one studies, respectively). These dissimilarities among ecosystems result from the focus of the few research teams involved in the field. This is particularly evident for papers published on the Atlantic forest, most of which have been written by the same team. Likewise, the numerous works conducted in Veracruz and Yucatán were impulsed by the strong Mexican ecology school.

Methodological Approaches

Descriptors of Resilience. The ecological descriptors used to estimate the resilience of palm populations and communities can be classified in four groups.

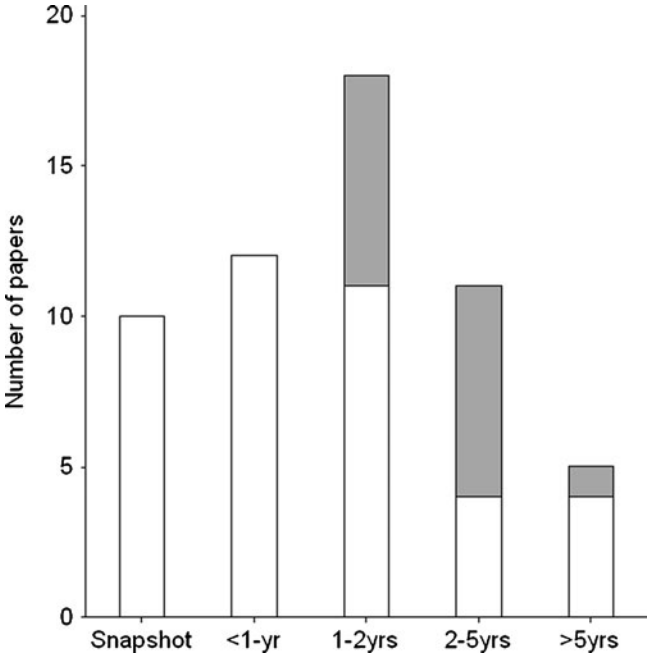

Fig. 2 Number of papers studying palm resilience in the Neotropics by (i) timescale (x axis), and (ii) use of transition matrices (grey bars)

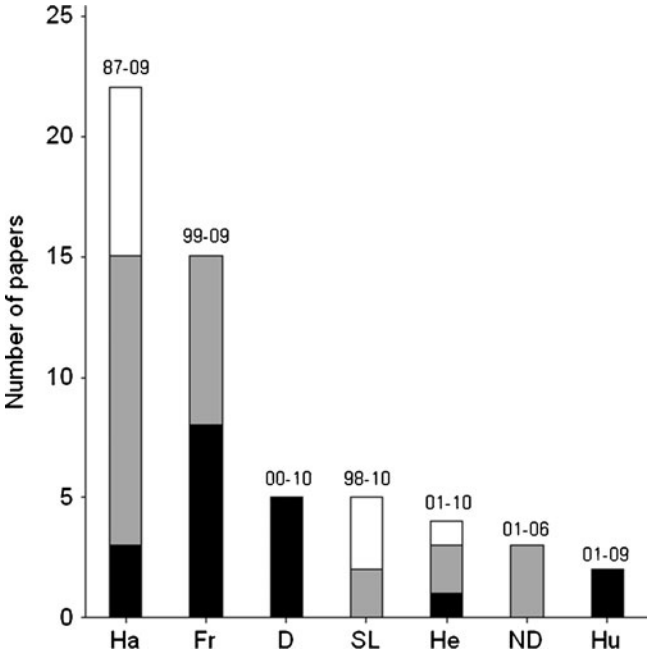

Fig. 3 Distribution of articles addressing palm resilience in the Neotropics by (i) type of disturbance (Ha: harvest; Fr: fragmentation; D: complete deforestation; SL: selective logging; He: herbivory; Hu: hunting; Fi: fire; ND: natural disturbance), and by (ii) resilience level (white bars: high; grey bars: medium; black bars: low). Above each bar: period during which papers were published

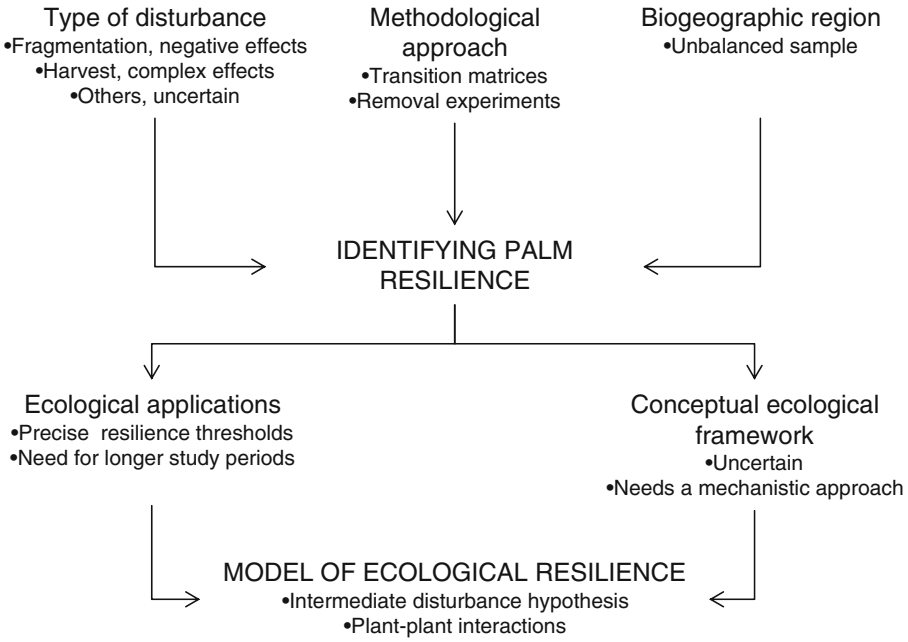

Fig. 4 Current knowledge on palm resilience in the Neotropics: what do we know? What do we need to develop in future researches?

(i) Productivity, with indices related to biomass and/or growth (e.g. Sampaio et al., 2008), percentage of plant damage (e.g. Chazdon, 1991), and density of individuals (e.g. Svenning, 1998); (ii) reproduction, with indices related to reproductive output (e.g. Bonjorne de Almeida & Galetti, 2007), seed density and/or dispersal (e.g. Berry et al., 2008), and sex ratio among adults (e.g. Barot et al., 2005); (iii) population dynamics, with indices of survival (e.g. Moegenburg & Levey, 2003) and demographic structure (e.g. Freckelton et al., 2003); (iv) species richness, which applies for studies at the community-level.

Selecting one or several resilience descriptors depends on the objective of the study. Studies aiming at increasing economical gain through harvest have considered descriptors of productivity (e.g. number of shoots; Pulido & Caballero, 2006; Pulido et al., 2007), while studies with a focus on population conservation have choosen descriptors of population dynamics (e.g. transition matrix), reproductive output (e.g. seed dispersal; Bonjorne de Almeida & Galetti, 2007), or species presence/absence at the community level (e.g. Svenning, 1998; Baez & Balslev, 2007).

The outcome of these descriptors is variable and a common trend is that those related to growth more likely demonstrate resilience than those related to reproduction (Chazdon, 1991).

Genetic descriptors of resilience include spatial or temporal comparison of genetic diversity (among sites with different degree of disturbance and recovery, or among successive generations) and measures of gene flow (Gaiotto et al., 2003; Sezen et al., 2007).

Population or Community Level. Ecological studies also generally focus on a particular species with keystone properties on the ecosystem (e.g. *Euterpe edulis*, Fadini et al., 2009; *Ceroxylon echinulatum*, Anthelme et al., 2011; *Mauritia flexuosa*, Holm et al., 2008). Among the studies reviewed here, only six study palm resilience at the community level, i.e. comparing the effects of disturbance on at least two palm species (Table 1). Although palms, as a distinctive taxonomic group, may behave relatively similarly when compared to other taxa and can thus be treated as a single entity (Norden et al., 2009), resilience levels can be very different among palm species under similar disturbance regime, such as selective logging (Svenning, 1998) or habitat fragmentation (Fleury & Galetti, 2004, 2006; Baez & Balslev, 2007), especially when comparing different spatial scales (Scariot, 1999). Therefore, direct comparisons of palm resilience through studies at the community level probably deserve closer attention in future research for a better understanding of the variability of palm responses to disturbances.

Genetic studies of palm resilience are all at the population level, and are limited to a few case studies (*Euterpe edulis*, Galetti et al., 2006; *Iriartea deltoidea*, Sezen et al., 2007). Some studies compare different species but not in a context of disturbance, so that interspecific differences in resilience abilities are only hypothesized (Luna et al., 2005, 2007).

Time Scale. Snapshot studies, short-term studies and long-term studies using permanent plots each have their own advantages and applications in ecology (see Stohlgren, 2007 for a review). A general consensus is that long-term studies are underrepresented in ecology (e.g. Brooker et al., 2008), especially because they require the development of intensive protocols. Nevertheless, papers exploring palm responses to disturbance on a time-range exceeding two years are relatively common in our sample (29% of the total) and surprisingly more frequent than snapshot studies (18%). This may be explained (i) by the high portion of papers studying the effects of harvest, that frequently develop in situ experiments comparing a control with various treatments (e.g. leaf removal, Anten et al., 2003) over several months or years, and (ii) by the frequent use of transition matrices (50% of the papers reporting a study of at least two years; Fig. 2). Data collection for constructing transition matrices requires a relatively long period to provide consistent predictions on the demographic structure and dynamics of palm populations. These data provide precise results for management purposes (e.g. Bernal, 1998; Holm et al., 2008). However, the fact that only a few studies consider periods over five years (9% of the sample, Fig. 2; but see Brum et al., 2008) might question the consistency of the results for slow growing palms. Data at longer temporal scales are required in future research (Endress et al., 2006).

Another specific feature of studies on palm resilience is the relatively high proportion of experimental studies, which also necessitate observations over several years (46% of the sample, Table 1). As for transition matrices, this approach, largely applied in the study of harvest effects (experimental removal of leaves, fruits or shoots), generates very precise results for management purpose (e.g. Mendoza et al., 1987; Calvo-Irabién et al., 2009).

Data on Microenvironment and on Physiological Responses to Disturbance. The distribution of tropical American palms has been shown to be highly sensitive to variations of the microenvironment (Svenning, 2001; Andersen et al., 2010).

Although transition matrices and experimentations provide a strong basis for the evaluation of individual and population resilience, the rarity of information on the microenvironment and on the morphological or physiological response of target species to disturbances (but see Anten et al., 2003; McPherson & Williams, 1998; Siebert, 2000; Zuidema et al., 2007), limits the interpretation of results in terms of mechanisms, thus preventing the shift from pattern to process analyses.

Disturbance Drivers

Harvest and, to a lesser extent, habitat fragmentation, have been the most studied disturbances affecting palms in tropical America (Fig. 3). Consequences of clearcutting (regeneration in pasture, secondary succession) and of selective logging on palms have been much less studied. The effects of hunting, fire, and natural disturbances on palm resilience are clearly understudied although being widespread causes of population alteration.

Deforestation. Both fragmentation and clearcutting were shown to deeply alter the structure and the dynamics of palm populations (Fig. 3), either directly or indirectly. Fragmentation has in most cases a negative impact on the demography of palms in remnant habitats (Scariot, 1999; Benitez-Malvido & Martinez-Ramos, 2003). Mechanisms underlying these negative effects of habitat fragmentation include higher competition with secondary forest species (Arroyo-Rodriguez et al., 2007), especially at the boundaries between forests and deforested areas. This negative edge effect at the community level (Baez & Balslev, 2007), may also impact palm dynamics through higher light intensity, altered distribution of dispersers and pollinators and mechanical disturbance such as increased numbers of tree-falls. However, a population study identified more complex effects, with a positive edge effect of habitat fragmentation on the density of saplings and adults in *Oenocarpus bacaba* (Brum et al., 2008). Therefore, studies at the community level have demonstrated an overall negative edge effect on palm fitness, but some species do benefit from this type of disturbance.

Fragmentation has been shown to indirectly affect palm demography negatively, (i) by reducing the density/diversity of pollinators available to *Astrocaryum mexicanum* (Aguirre & Dirzo, 2008), and (ii) more commonly by reducing the density/diversity of seed dispersers. Due to limitations in seed dispersal consecutive to fragmentation, several tropical American palms are considered to be in danger of extinction (e.g. Galetti et al., 2006), especially because of the occurrence of genetic inbreeding (Clement et al., 2009). However, palms producing fruits dispersed by a wide range of vertebrates may be less sensitive to such effects. Bird and bat dispersal may remain effective in a fragmented forest landscape because these animals can fly over pasture and maintain genetic connectivity between forest fragments through seed dispersal (Sezen et al., 2007). The size effect of forest fragments was analyzed

in several tropical American ecosystems and revealed complex effects of microhabitats that deserve further research (Scariot, 1999; Fleury & Galetti, 2004, 2006; Aguirre & Dirzo, 2008; Wang, 2008).

The direct effects of clearcutting have been less studied than the effects of fragmentation (Fig. 3). *Attalea speciosa*, which establishes easily and sometimes becomes invasive in clearcut areas and pastures, starts flowering and fruiting at lower height and has irregular timing between males and females when it grows outside the forest (Barot et al., 2005). In Ecuador adults of *Ceroxylon echinulatum* and *Attalea colenda* resist the abiotic stress caused by deforestation, but seedlings cannot survive and populations in pastures do not regenerate (Borchsenius et al., 1998; Anthelme et al., 2011).

Harvesting of Palms and Palm Parts. The high number of studies published since 1987 that investigate effects of harvest on palm populations (Mendoza et al., 1987) reflects the high economic value of the palm family and its importance as provider of NTFPs. Target material is primarily leaves (e.g. Pedersen, 1996; Svenning & Macía, 2002; Valverde et al., 2006; Martínez-Ramos et al., 2009), but also palm heart (Freckelton et al., 2003), seeds (Bernal, 1998; Holm et al., 2008), fruits (Moegenburg & Levey, 2003; Holm et al., 2008), shoots (Siebert, 2000; Escalante et al., 2004), stems (Anderson & Putz, 2002), or even sap (Wright & Duber, 2001; Galetti et al., 2006).

The sustainability of various harvesting modes is the purpose of most papers, following Holm's et al. statement (2008) that the challenge for NTFPs is finding the harvest level that will supply enough income to forest dwellers while at the same time maintaining population viability of harvested species. Overall, available data tend to detect a complex effect of harvest intensity on palm growth, varying from positive (*Sabal spp*., Martínez-Ballesté et al., 2008; *Desmoncus orthacanthos*, Siebert, 2000) to neutral (*Chamaedorea elegans*, Martínez-Ramos et al., 2009) and negative (*Geonoma deversa*, Flores & Ashton, 2000), while effects on reproductive output are found to be systematically negative (*Geonoma deversa*, Flores & Ashton, 2000; *Chamaedorea radicalis*, Endress et al., 2004a,b; *Chamaedorea elegans*, Martínez-Ramos et al., 2009). Effects vary according to the percentage of individuals harvested, with some precise thresholds proposed in various studies (86% of seeds of *Phytelephas seemannii*, Bernal, 1998; 40% of shoots of *Desmoncus orthacanthos*, Escalante et al., 2004; 22.5% of *Mauritia flexuosa* females harvested in fruits every 20 years, Holm et al., 2008; 33% of leaves of *Astrocaryum mexicanum* harvested, Mendoza et al., 1987; 30% of leaves of *Thrinax radiata* harvested, Calvo-Irabién et al., 2009). Harvest effects also vary according to the life-stage harvested: harvesting juveniles of *Astrocaryum mexicanum* may lead to population decline more rapidly than harvesting adults (Mendoza et al., 1987). Harvesting reproductive adults was shown to enhance sustainability in *Euterpe edulis* (Freckelton et al., 2003), while conserving reproductively active individuals of *Chamadorea radicalis* favors sustainable harvest (Endress et al., 2006). Selecting mature leaves lead to a better sustainability in some species (*Sabal spp*., Martínez-Ballesté et al., 2008), and can enhance leaf production up to 30% in other species (*Astrocaryum mexicanum*, Mendoza et al., 1987), evidencing the crucial role of life history traits for resilience. Leaf production is an important concern when considering that some palms such as

Ceroxylon echinulatum (Anthelme et al., 2011), *Prestoea acuminata* (Bonilla & Feil, 1995) or *Euterpe edulis* (Freckelton et al., 2003) are specifically harvested for their young leaves. Some species are particularly resilient to harvest, regardless of life-stage or leaf maturity, such as *Desmoncus orthocanthos* (Siebert, 2000) and *Sabal* spp. (Martínez-Ballesté et al., 2008). Finally, indirect effects of harvest include negative effects on seed dispersers through fruit removal (*Euterpe oleracea*, Moegenburg & Levey, 2003).

Harvest is certainly the best-known type of disturbance when considering its effects on the resilience of tropical American palm populations. The variety of responses described indicates highly species-specific behaviors. Compared with fragmentation, clearcutting, or browsing in *Chamaedorea radicalis* (Endress et al., 2004a), harvest can more easily be managed as to ensure population viability.

Harvest has been shown to be directly related to the level of poverty of local inhabitants (*Chamaedorea sp*., Lopez-Feldman & Taylor, 2009), as well as positively correlated with the remoteness of markets where palm products can be sold (Byg et al., 2007). Therefore, limiting non-sustainable harvesting could also be achieved by acting on socio-economic factors.

Other Disturbances. Selective logging is one of the most common and widespread causes of disturbance in tropical America but it has been little studied with respect to its impact on palm populations (Fig. 3). Two studies were carried out in tropical mountain cloud forests in northwestern Ecuador, as a response to concerns about high rates of deforestation in this region (Svenning, 1998; Anthelme et al., 2011). Both studies suggest that resilience to selective logging (partial clearing) is relatively high. However, the outcome of resilience may be strongly species-specific, as indicated by studies at the community level (Svenning, 1998). Selective logging may often be associated with habitat fragmentation, thus displaying antagonistic effects on palm resilience (positive effect due to selective logging but negative effect by fragmentation; Anthelme et al., 2011). For these reasons, more data are needed in this field.

Herbivory tends to negatively affect the fitness of tropical trees (D'Angelo et al., 2004). However, the effects of domestic herbivores are often entangled with the effects of clearcutting (e.g. Barot et al., 2005). The few studies exploring the separated effects of domestic herbivores on palm dynamics found a negative impact of browsing on the survival of seedlings, juveniles and young adults (Endress et al., 2004a). Considering that deforestation in tropical America is often followed by pasture development (e.g. Wang, 2008), this factor deserves more attention in future research on palm resilience.

The effects of hunting and fire are part of the altered dynamics of tropical trees, especially when associated with the effects of habitat fragmentation caused by large-scale deforestation (Wright & Duber, 2001; Wang, 2008). Hunting is a direct and severe cause of defaunation in tropical forest (Siren et al., 2004; Zapata et al., 2009). Although hunting has been shown to affect negatively the resilience of palm populations (Fig. 3), studies on this aspect remain scarce.

The effects of fire have been even less addressed in tropical America. A study on *Attalea humilis* revealed an intermediate resilience level for this species which is adapted to fire (Souza & Martins, 2004). However, a study in Australia on

Ptychosperma macarthurii showed various negative indirect effects of fire on palm resilience, especially when associated with other disturbances (Liddle et al., 2006). Another natural disturbance, flooding, was shown to have a medium impact on palm resilience, its differential effect among species possibly explaining the distribution of sympatric species (Pacheco, 2001).

A single study addresses the effects of natural or global disturbances on the fitness of palm populations, through the combined effects of ENSO (El Niño Southern Oscillation) and experimental defoliation on the fitness of *Chamadorea elegans* (Martínez-Ramos et al., 2009). These authors suggest that strong episodic disturbances not related with deforestation or harvest may strongly alter palm demographic structure in tropical forests. More generally, global change combined with habitat fragmentation is hypothesized to affect the density and basal area of tropical tree species, and the alteration of tree communities in undisturbed Amazonian forests might be due to rising atmospheric CO_2 concentrations (Laurance et al., 2004). Therefore, there is a basic need for long-term experiments designed to disentangle the direct anthropogenic effects, effects of global change, and periodic global disturbances such as ENSO on the fitness of tropical American palms.

Broad Scale and Long-Term Factors Influencing Palm Population Dynamics

The effects of broad-scale and long-term factors on the dynamics of tropical American palm populations have been poorly explored, although this information is crucial to predict future adaptation and evolution of palm populations in a changing environment.

The distribution range of species has consequences for their populational diversity and vulnerability. Tropical American palm species in general present great variation in range sizes. Species such as *Geonoma deversa*, *Oenocarpus bataua* or *Attalea maripa* are widely distributed, whereas others, for example *Geonoma tenuissima* or *Cryosophila macrocarpa* are restricted to very small areas (Henderson et al., 1995; Borchsenius et al., 1998; Bjorholm et al., 2005; Galeano & Bernal, 2010). Vicariance events of geological nature, episodic long distance dispersal, past climate changes and contemporary climate and soils determine the spatial distribution patterns of palm species at regional and continental scales (Clark et al., 1995; Vormisto et al., 2004; Bjorholm et al., 2005, 2006; Montúfar & Pintaud, 2006).

Dispersal across the Andes has been studied in two species in Ecuador. Trénel et al. (2008), found a strong geographic structure in the genetic diversity of *Ceroxylon echinulatum*, with four highly differentiated subpopulations, two on either side of the Andes, with evidence of trans-Andean dispersal of Quaternary age (>0.6 MY). Montúfar (2007) detected little genetic divergence between populations of *Oenocarpus bataua* on either side of the Andes, suggesting a persistence of cross-Andean gene flow until at least late Pleistocene. In the western Amazon basin, *Oenocarpus bataua* populations separated by 200–400 km showed significant isolation by distance and corresponding low rates of gene flow (Montúfar, 2007). Similarly, high levels of genetic differentiation were described for 11 populations of

Euterpe edulis separated by 40–1700 km in the Atlantic rainforest, a pattern explained by historical fragmentation of the ecosystem (Cardoso et al., 2000).

The data suggest that the genetic diversity of many palm species with widespread or fragmented distribution is influenced by both isolation and current or relatively recent genetic connectivity at long distance or across barriers (Cibrián-Jaramillo et al., 2009).

Effects of late Quaternary climatic variations on the population dynamics of palms have been studied in one species in French Guyana, *Astrocaryum sciophilum* (Charles-Dominique et al., 2003). The patchy distribution of this species under a continuous forest cover could be explained by a very slow response to environmental changes. The forest habitat has undergone repeated disturbances, in particular recurrent fires during the Holocene, and the extant populations have been slowly expanding from refuge nuclei over the past 5000 years. With an average delay to sexual maturity of 170 years, and a mean colonization rate of 2.3 m per year, this species is not likely to reach a populational equilibrium, because its dynamic is slower than that of environmental fluctuations.

The pre-historical and historical role of humans on the distribution and abundance of palms in tropical America is poorly understood and probably underestimated. There are evidences of human disturbance in Amazonia throughout the Holocene (Bush et al., 2000). Some areas were densely populated and intensively managed in pre-Columbian times, until depopulation ca. 1600–1700 followed by extensive forest regrowth (Heckenberger et al., 2003). Balée (1989) suggested that 11.8% of the 3.3 millions of square kilometers of *terra firme* forest of the Brasilian Amazon is represented by anthropogenic forest of palms, vines and bamboo. Patches of *Elaeis oleifera* in the central-western Amazon basin are often associated with *terra preta do indio*, soils rich in organic matter and carbonized wood that indicate ancient settlements (Henderson, 1995). Some vernacular names of palms refer to ancient uses that are now totally abandoned. Some of these uses are likely to have impacted palm populations in the past, such as starch extraction from *Iriartea* trunks (Bernal et al., 2007). The diversity of palm archeological remains in the New World indicates a long history of use, management and domestication of palms (Morcote-Ríos & Bernal, 2001).

Role of Life History Traits in Palm Population Dynamics and Resilience

Life history traits depict the adaptation of palms to their environment (Kahn & de Granville, 1992), and constrain their response to disturbance.

Vegetative Architecture

Considerable variation exists in palm vegetative architecture, depending on absence or presence and extant of basal branching (clumped, stoloniferous, rhizomatous palms), absence or presence and size of stilt roots, overall size of the palm (from 50 cm to 50 m), relative size of trunk and leaves, stem characters (subterranean, aerial, self-supporting or lianescent, ramified or not), growth patterns including type of establishment phase (Dransfield, 1978; Tomlinson, 1990; Tomlinson et al., 2011).

This morphological variability allows palms to occupy a wide range of niches in the tropical American realm (de Granville, 1992; Kahn & de Granville, 1992).

Some vegetative characteristics have a direct effect on individual or population resilience. For example, the 'saxophone growth' type (Tomlinson, 1990), which is characterised by a geotropic growth of the trunk in the early stages of development, ensures an effective underground protection of the apical meristem of juvenile palms and acaulescent adults. This strategy allows palms to resist the effects of falling branches and palm leaves in the forest understory, a major cause of sapling mortality in tropical forests (Aide, 1987), and also ensure survival after clearcutting of the forest and fire, resulting in high survivorship of individuals (Charles-Dominique et al., 2003). Various *Attalea* species with 'saxophone' growth, which are relatively scarce in primary rainforest, become invasive in pastures, eventually producing monodominant stands over extensive areas (Barot et al., 2005).

Stilt roots also have important implications on the ecology and resilience of palms that develop these structures (Schatz et al., 1985). The highly specialized stilt-root palm *Socratea exorrhiza* lacks an acaulescent establishment phase and is able to elevate itself in shade at the young stage with minimal investment in trunk building, progressively consolidating its architecture with increasing energy availability while reaching higher understory strata (Hogan, 1986). The palm has a high survival rate at all stages since it resists very efficiently the effects of branch fall. Impacted palms are partially derooted, fall, re-root below the leaf crown and re-establish (Bodley & Benson, 1980).

Clonality is another important adaptative strategy. In the Amazon forest in particular, some species like *Lepidocaryum tenue*, *Iriartella stenocarpa*, *Wettinia drudei*, *Bactris bifida* or *Bactris bidentula* can completely dominate the forest understory through a stoloniferous or rhizomatous growth (Henderson, 1995). Vegetative reproduction also allows individual recovery upon trunk harvest (Chazdon, 1991; Siebert, 2000), after forest clearcutting, herbivory damages (Sampaio & Scariot, 2010) or natural disturbance (de Steven, 1989). Clonality allows particular mechanisms of individual resilience through physiological integration of ramets, allowing resources translocation as a response to partial damages to the palm (Mendoza & Franco, 1992).

Palm trunks often accumulate large quantities of energetic reserves in various forms of carbohydrates (Tomlinson, 1990). Starch reserves play an important role in the individual resilience under various natural and anthropogenic conditions, like leaf harvesting, and act even at the seedling stage (McPherson & Williams, 1998). However, carbohydrate resources have little direct use in tropical America and are therefore not a significant cause of palm destruction. Only a few indigenous groups extract starch from *Mauritia* or *Manicaria* (Heinen & Ruddle, 1974; Wilbert, 1976) and the sweet medula of *Ceroxylon* is occasionaly used to feed pigs (Pintaud & Anthelme, 2008).

Reproductive Traits

Flowering and Sexual Strategies. The morphology of the palm flower is rather unspecialized (Dransfield et al., 2008). A typical palm flower is small (1–2 cm), with 3 imbricate sepals, 3 valvate petals, six stamens or staminodes, and 3 uniovulate

carpels or a trifid pistillode. Flowers are arranged into clusters (sympodial, dyad, triad, acervulus), well exposed and relatively open to pollinators (Henderson, 1986; Silberbauer, 1990; Dransfield et al., 2008).

Spatial and temporal distribution and maturation of sex organs are very important factors involved in the gene flow dynamics of plant species. A number of life history strategies, discussed below, enhance genetic flow and promote genetic diversity (Loveless & Hamrick, 1984).

Palms are generally monoecious, although the hermaphroditic flower is likely to be the ancestral condition, present in five genera of Calamoideae and 20 genera of Coryphoideae (Dransfield et al., 2008), while bisexuality is vestigial in most functionally unisexual flowers (Adam et al., 2005; Daher et al., 2010), except in staminate flowers of Phytelepheae (Barfod & Uhl, 2001). In tropical America, palms with hermaphroditic flowers include 14 genera of Coryphoideae, mostly from the Caribbean region. Dioecy is relatively uncommon with only ten genera with this feature (e.g. Mauritiinae, Ceroxyleae). Dioecy implies different strategies of resource allocation depending on the sex of the plant, and consequently differential selective effects on male and female plants (Cepeda-Cornejo & Dirzo, 2010). Arecoideae is the most diverse palm subfamily in tropical America with 39 genera, mostly monoecious, with the exception of the dioecious *Chamaedorea* and *Wendlandiella*. In general terms, monoecy is a common floral strategy in tropical forests. Monoecy is a versatile strategy that allows all variation in the autogamy/allogamy ratio from self-pollination to functional dioecy, permitting individual and populational reproductive plasticity and adaptation of species to a wide range of environmental conditions (Adam et al., 2005; Barot et al., 2005). Protogyny and protandry are the underlying mechanisms favouring allogamy in monoecious palms. Both conditions are frequent in tropical American palms, such as in Bactridinae, with *Aiphanes* being protandrous (Listabarth, 1992b), while *Acrocomia*, *Astrocaryum*, *Bactris* and *Desmoncus* are protogynous (Scariot & Lleras, 1991; Listabarth, 1992b; Henderson et al., 2000). Protogyny is common in Cocoseae in general, and it is also found in *Cryosophila*, and may have evolved as a response to beetle pollination (Henderson, 1986; Henderson et al., 2000). Protandry characterizes groups like Euterpeae and Geonomateae (Ervik & Feil, 1997; Listabarth, 1993).

Palms show a great diversity in pollination syndrome but are predominantly entomophilous and beetles-pollinated (Henderson, 1986; Silberbauer, 1990). Early botanists thought that palms were wind pollinated (reviewed by Henderson, 1986). While anemophily has been confirmed in several palms (Listabarth, 1992b; Luna et al., 2005; Savolainen et al., 2006), a large body of data on palm entomophily has accumulated over the last decades (e.g. Henderson, 1986; Anderson et al., 1988; Barfod, 1988; Silberbauer, 1990; Olesen & Balslev, 1990; Ervik, 1993; Listabarth, 1992a, 1993, 1996; Bernal & Ervik, 1996; Couturier et al., 1997; Ervik et al., 1999; Otero & Oyama, 2001; Nuñez et al., 2005; Nuñez & Rojas, 2008). Three entomophilous syndromes are recurrent among palms: (i) bee pollination (melliophily), involving the genera *Melipona*, *Apis* and *Trigona*; (ii) beetle pollination (cantharophily), involving mostly Nitidulidae, Staphylinidae and Curculionidae; and (iii) fly pollination (myophily), involving families Calliphoridae, Syrphidae, and Drosophilidae, characteristic of some understory palm species. Additionally, a mixed syndrome named *insect-induced wind pollination* has been proposed for the

understory palm *Chamaedorea pinnatifrons*, in which insects could induce the release of small clouds of pollen in the forest atmosphere (Listabarth, 1992a).

Palms have developed various morphological and physiological adaptations to enhance insect pollination. Palm flowers generally produce volatile organic compounds (VOCs) attracting insects. A chemical survey carried out on tropical American palms showed great diversity in floral scent composition, with variations depending on pollination syndromes (Knudsen et al., 2001). Differentiation in floral odours could play a role in genetic divergence and speciation in palms. Examples of floral odours differentiating closely allied taxa include the genera *Ammandra* and *Phytelephas* (Ervik et al., 1999), sympatric species of *Phytelephas* (Ervik et al., 1999) and *Geonoma* (Knudsen, 1999a,b, 2002). It is not clear, however, if floral scent divergence is a cause or a consequence of speciation, merely maintaining reproductive isolation in the second case (Knudsen, 1999b). Floral thermogenesis is also widespread in the palm family (Kuchmeister et al., 1993; Ervik & Barfod, 1999; Nuñez et al., 2005; Nuñez & Rojas, 2008). Thermogenesis enhances evaporation of floral scent, increasing attractiveness to insects, mostly beetles (Thien et al., 2000) and represents a direct energetic reward (Ervik & Barfod, 1999). Nectar is another important and common insect reward of palm flowers. Nectar is produced mainly from septal nectaries, the most common type of nectary in monocotyledons (Schmid, 1983; Stauffer et al., 2002).

Seed Dispersal. The morphology of palm fruits is variable (Dransfield et al., 2008), but can be classified as either berry (fleshy or fibrous mesocarp, one seed and thin endocarp) or drupe (endocarp slerotic and thick). The palm fruit is generally ovoid to ellipsoidal and with a diameter varying between 4.5 mm and 50 cm. Both mesocarp and endosperm provide food for animals, and the texture of the mesocarp and the seed size determine modalities of dispersal (Tomlinson, 1990).

Large palms in the genera *Attalea*, *Astrocaryum*, *Euterpe, Oenocarpus*, *Mauritia*, *Roystonea* or *Ceroxylon* produce numerous large inflorescences that provide numerous large fruits. These palms are key resource for frugivorous species, providing fruits year-round (Goulding & Smith, 2007). In general, palm communities produce large amounts of organic matter annually in the form of fruits and seeds (Kahn & de Granville, 1992).

Palm dispersal shows a great diversity of mechanisms in relation to the high variability of fruit morphology, but zoochory is the dominant dispersal mode in the palm family (Zona & Henderson, 1989).

Fleshy or fibrous, lipid-rich mesocarps of small to medium-sized palm fruits are attractive to birds (Snow & Snow, 1978; Tannenbaum & Wrege, 1978; Moraes, 1991; Bühler, 1993; Galetti & Guimarães, 2004), bats (Lobova et al., 2009), non-flying mammals (Smythe, 1986, 1989; Bodmer, 1991; Hoch & Adler 1997; Norconk et al., 1998), and fish (Piedade et al., 2006). Fruits with a fibrous mesocarp and an endosperm protected by a thick and hard endocarp, like those of *Attalea* and *Astrocaryum*, or with a very hard endosperm as in *Aphandra*, are important food resources for rodents, agouties and pacas (Forget, 1991, 1997; Beck & Terborgh, 2002; Silvius & Fragoso, 2003; Boll et al., 2005). Peccaries are generalist palm fruit consumers and contribute to the dispersal of a high number of palm species in tropical American forests (Beck, 2006). Tapirs are also important fruit consumers, as

are primates (Norconk et al., 1998; Henry et al., 2000; Olivier et al., 2000; Fragoso et al., 2003; Link & Di Fiore, 2006). Dispersal by reptiles (saurochory) has been reported for *Serenoa* (Liu et al., 2004).

Zoochory plays a fundamental role in the long distance seed dispersal in palms. The fruits of *Oenocarpus bataua*, *Euterpe precatoria* and some species of *Bactris* are consumed and dispersed by the oilbird (*Steatornis caripensis*), that can travel up to 73.5 km in one day and colonies of oil birds can transport millions of palm seeds annually (Tannenbaum & Wrege, 1978; Snow & Snow, 1978; Holland et al., 2009). Evidence of long distance seed dispersal has also been reported for *Attalea phalerata* by crested caracaras (*Caracara plancus*; Galetti & Guimarães, 2004). The role of bats as long distance dispersers has been little studied in tropical American palms, but the literature reports that about 15 palm species are dispersed by bats in tropical American forests (chiropterochorous syndrome; see Lobova et al., 2009), and additional new data from French Guiana suggest that most palm species from Central French Guyana are potentially dispersed by bats, at least occasionally (Lobova et al., 2009). Research on long distance dispersal by bats in Indonesia suggested that Old World fruit bats have the potential to disperse small seeds over hundreds of kilometers (Shilton et al., 1999). Lobova et al. (2009) suggests that bats are effective dispersers because they are (i) selective and disperse mature seeds, (ii) the majority of fruits are taken away from the parent tree, (iii) they usually defecate small diasporas in flight with an effective dissemination over large areas, and (iv) the digestive systems of bat do not destroy seeds.

The seed dispersion of riparian palms like *Bactris riparia*, *Astrocaryum jauari*, *Leopoldinia pulchra*, has been poorly explored, although ichtyochory (fish dispersion) could be an optimal dispersal mechanism for many species of *várzea* and *igapó* forest. The spiny palm *Astrocaryum jauari* forms oligarchic populations on flooded areas along the Amazonian rivers. Dispersal studies in the central Amazon basin reported that ripe fruits of *A. jauari* were eaten by 16 fish species, some of them without breaking the seed (Gottsberger, 1978; Piedade et al., 2006). *Socratea exorrhiza* has also been associated to the ichthyochory syndrome (Gottsberger, 1978). Hydrochory is probably another important way of seed dispersal in riparian palms that often form oligarchic populations close to rivers and lakes (Goulding & Smith, 2007). Hydrochory (including seed transport by floating islands and large debris) may be sporadically involved in long-distance seed dispersal. For example, the palm flora of Marajo Island, in the Amazon estuary, comprises palm species that originate in the western and central regions of the Amazon basin and it is therefore assumed that palm diversity in Marajo is influenced by river dispersal (Henderson et al., 1991).

Humans are also important dispersers of palm seeds in tropical forests. In particular, local people who move across the Amazon forest transport palm fruits as food reserve during these travels. The distribution of palm species like *Astrocaryum aculeatum* is certainly influenced by humans (Kahn & Moussa, 1995, 1999). The reach of human movements in the Amazon basin is highly variable and can vary from few to thousands of kilometers. Additionally, the modern regional trade of non-timber forest products is structured around convergence centers like Iquitos markets in the Peruvian Amazon (Mejía, 1992; Balslev et al., 2008), from where a percentage of the genetic diversity of the edible palm species can be dispersed again to other places through fruit purchase.

Gene Flow Through Pollen and Seed Dispersal and its Alterations. Gene flow is an essential force underlying the genetic connectivity among natural populations at all scales. Intense and widespread gene flow will act as a homogenizing force preventing genetic divergence and subpopulation structuring (Slatkin, 1985), while restricted gene flow will favour population isolation and, ultimately, speciation (Loveless & Hamrick, 1984; Slatkin, 1985; Lowe et al., 2004).

In natural plant populations with sexual reproduction, the equilibrium between homogenization and heterogeneity of the genetic pool depends primarily upon the dynamics of pollen and seed dispersal (Aldrich & Hamrick, 1998; Godoy & Jordano, 2001; Hardesty et al., 2005, 2006). Both pollen and seed dispersal are constrained by a number of ecological factors including density and aggregation of individuals, effects of habitat heterogeneity (Vormisto, 2000; Vormisto et al., 2000; Svenning, 2001) and predation (Janzen, 1970), all of which result in the establishment of descendents (Luna et al., 2005). For plant populations, total gene dispersal is composed of pollen dispersal (pollination) and seed dispersal; the latter contribute twice as much to gene dispersal because pollen is haploid while the embryo is diploid (Slatkin, 1985; Hamilton, 1999).

Whereas pollen flow and subsequent pollination are directly involved in the formation of the genetic identity of the next generation individuals (Proctor et al., 1996), seed dispersal shapes the overall distribution of genes within and among populations.

The use of genetic markers for paternity studies has made it possible to explore patterns of pollen flow and such studies have revealed that a significant fraction of tropical trees are outcrossed, with relatively long-distance pollination by insects playing an important role in gene flow (Stacy et al., 1996; Latouche-Hallé et al., 2004).

Seed dispersal is also a strong force structuring plant communities and their genetic diversity (Loveless & Hamrick, 1984; Wenny, 2001; Wyatt & Silman, 2004; Tristram & Plotkin, 2006). Dispersal favors the escape of seeds and seedlings from high mortality areas caused by distance or density-dependent factors near parent trees (Escape hypothesis: Howe & Smallwood, 1982; Clark & Clark, 1984). The escape strategy increases the survival rate of genotypes far away from the parent trees reducing the probability of inbreeding for the next generations. Studies carried out with *Iriartea deltoidea* (Sezen et al., 2007) suggest that seedling recruitment is related to efficient dispersal since more than 70% of seedlings were dispersed at least 50 m away from the parent trees. A seed with lower dispersal limitation has a higher probability to colonize new habitats with patchy distribution such as light-gaps in forest (Colonization hypothesis; Augspurger, 1984). Colonization of new habitats starts with the migration and establishment of few individuals in these areas. The genetic pool of these new populations will be dependant on the founder effect, implying limited initial diversity and high genetic drift creating a strong bottleneck (Lowe et al., 2005). A genetic study of founder populations of *Iriatea deltoidea* in secondary forest (Sezen et al., 2007) illustrated the low genetic diversity of individuals in secondary forest in comparison with individuals in adjacent old-growth forest, and the persistence of this effect through several generations, in lowlands of Costa Rica.

A particular modality of seed dispersal called directed, or targeted, dispersal was proposed by Wenny (2001). It occurs when a dispersal agent deposits seeds in

suitable areas for their germination and development, and it assumes a non-random process among plant, dispersers, and areas (Wenny, 2001). The directed seed dispersal by the frugivorous bird *Cephalopterus penduliger* (umbrellabird) resulted in a significantly higher genetic diversity of seedlings of *Oenocarpus bataua* in targeted deposit areas of the tropical forest of north-western Ecuador, compared to other sites (Karubian et al., 2010). Non-random dispersal—expressed as seedling patches across the forest—have been reported for small and medium size-seeded palms including *Iriartea deltoidea, Oenocarpus bataua* and *Euterpe edulis* (Pizo, 2001). The behaviour of the vertebrate seed dispersers and the ecology of the habitat are key factors shaping these dispersal and genetic patterns (Forget, 1997; Svenning, 2001). In some cases, dispersal enhances germination after gut passage in vertebrates (Henry et al., 2000; Fragoso et al., 2003).

Anthropogenic effects (logging, harvesting, fragmentation, habitat degradation) also reduce the rate of outcrossing, favouring high rates of self-fertilization, and genetic drift among isolated and reduced sub-populations (Hamilton, 1999; Cardoso et al., 2000; Sezen et al., 2007). Where ecological conditions are altered, such as in open forest, insects face increasing distances to cover between trees while suffering major exposure to sun radiation, elevated temperatures and lower humidity, thus reducing their efficiency as pollinators. Alteration of habitat ultimately results in reduction of pollinator abundance and diversity (Powell & Powell, 1987; Steffan-Dewenter & Tscharntke, 1999; Samejima et al., 2004; Brosi, 2009; Winfree et al., 2009; Dauber et al., 2010; Nayak & Davidar, 2010; Quintero et al., 2010). Studies in fragmented forests in Mexico revealed that arthropod fauna associated with inflorescences of *Astrocaryum mexicanum* was negatively affected by habitat alteration, however without consequence on fruit set (Aguirre & Dirzo, 2008). In other contexts, pollen limitations can also impact fruit set in palms (Cunningham, 1996).

Increasing evidence supports the hypothesis that anthropogenic disturbance directly and indirectly induces the decline of insect pollinators (Potts et al., 2010). The decline of pollination services will affect the genetic structure of wild plant populations reducing levels of gene flow and genetic variation. These effects can results in inbreeding depression and consequently a reduction of the ability of plant populations to respond to short and long term environmental changes. Although wind could partially sustain gene flow, the effect of this vector is likely to be limited in most palm populations, especially of tropical forest understory, where palms are most diverse.

The sex ratio of populations can also be affected by human impact, either directly by destructive harvesting of female trees, as it is the case for *Mauritia* (Holm et al., 2008) or indirectly by differential survival between sex in disturbed environments like pastures, as for *Ceroxylon* (Anthelme, Sanín & Pintaud, pers. obs.). Plants of different sex also tend to behave differently under leaf harvest, with males being more resilient (Oyama & Mendoza, 1990).

Although various studies on the phenology of palm populations and communities have been conducted in tropical America (Croat, 1975; Beach, 1984; Myers, 1984; de Steven et al., 1987; Zona, 1987; Sist, 1989a; Ibarra-Manríquez, 1992; Peres, 1994; Henderson et al., 2000; Piedade et al., 2006), little attention has been paid to phenological alterations in disturbed environments. Barot et al. (2005) found phenological variation in *Attalea speciosa* when comparing populations in pastures,

dense secondary stands and primary forest. These modifications are likely to influence gene flow.

Demography and Genetics of Palm Populations

Role of Population Structure and Demography on Resilience Levels. Seedlings are often numerically dominant in the population structures of lowland tropical American forest palms, due to high seed production and high germination rates (Sist, 1989b; Sist & Puig, 1987). Mortality is high before the acaulescent juvenile stage, which is in general highly resilient. Therefore, demographic strategies of palms usually combine a high investment in reproduction with high survival of established individuals (Sampaio & Scariot, 2010).

Palms with a long, acaulescent establishment phase, and a long subcanopy to emergent reproductive phase, tend to have a U-shaped population structure due to the accumulation of juveniles and adults and the scarcity of subadults in phase of rapid trunk growth (Vallejo et al., 2004). Forms of extractivism that specifically target subadults, such as fiber extraction of *Astrocaryum chambira* (Coomes, 2004), although having a seemingly minimal impact on the forest, can truncate natural population dynamics by inhibiting adult recruitment. These bimodal population structures promote on the other hand positive responses to disturbance, including density increase in selectively logged forest. Many forest palm populations include numerous acaulescent juveniles in the establishment phase, that accumulate in the understory until a light gap provides them the necessary energy to build an aerial stem and reach sexual maturity (Kahn & de Granville, 1992). Acaulescent juveniles can maintain themselves almost indefinitely at this stage in the deep shade of the understory (Charles-Dominique et al., 2003). Artificial light gaps like those produced by selective logging can induce a massive growing burst of these juveniles and quickly convert them in a dominant subcanopy, canopy or emergent palm layer (Pintaud, 2006). Light-gap dynamics (Martínez-Ramos et al., 1988; Cintra & Horna, 1997), and other intermediate-level disturbances, either human-induced or natural, are probably very important in shaping aggregative distribution patterns of palms in forests, like *huicungales*, which are localized stands of subcanopy *Astrocaryum* species in the western Amazon basin (Vallejo et al., 2004).

Genetic Structure of Palm Populations. Wild palm populations tend to show high levels of genetic diversity. Genetic studies on palm populations of *Euterpe edulis* (Cardoso et al., 2000; Conte et al., 2003; Gaiotto et al., 2003), *Chamaedorea* spp. (Cibrián-Jaramillo et al., 2009; Luna et al., 2005; Luna et al., 2007), *Astrocaryum mexicanum* (Eguiarte et al., 1992), *Bactris gasipaes var. chichagui* (Couvreur et al., 2006), *Oenocarpus bataua* (Montúfar, 2007), *Ceroxylon echinulatum* (Trénel et al., 2008) have reported high levels of genetic variation in comparison to other tropical trees. Additionally, evidence of high allelic variation at SSR loci (short sequence repeat) has been found for *Attalea phalerata* (Choo et al., 2010), *Acrocomia aculeata* (Nucci et al., 2008) and *Oenocarpus bacaba* (Lepsch-Cunha et al., 2003). Exceptions to the pattern of high diversity were reported by McClenaghan & Beauchamp (1986) and Roncal et al. (2007). The former research suggested a low

allozymic variation in the long-lived *Washingtonia filifera* that was associated with recent colonization events. The latter work described low levels of genetic diversity on *Geonoma macrostachys* based on ISSR data (inter simple sequence repeats); these results were explained by technical limitations and sample design.

High genetic variation of palms could be explained by life history traits (high pollen and seed flows) and biogeographical history. High rates of gene flow in palms may have either positive or negative effects on population resilience. Gene flow facilitates recovery of genetic diversity during secondary forest dynamics (Sezen et al., 2007), but can also promote genetic pollution of wild populations closely allied to crops like *Elaeis guineensis* and *Bactris gasipaes*, in areas of sympatry of the wild and cultivated plants. In western Ecuador, genetic pollution of the wild *Bactris gasipaes var. chichagui* by the cultivated *B. gasipaes var. gasipaes* is likely to decrease fitness of natural populations by introgression of genes from the cultivated pool having a negative phenotypic impact (larger fruits maladapted to bird dispersal, decrease in drought resistance and shade tolerance). This genetic alteration is favored by the highly fragmented remnant habitat of the wild populations, with increased edge-effects with bordering fields of the palmito crop (Pintaud et al., 2008a).

Interpopulation genetic differentiation tends to be lower in palm populations than in other tropical trees. A genetic study, using microsatellite loci showed low genetic differentiation between two populations of *Euterpe edulis* isolated by 22 km in the Atlantic Rainforest (Gaiotto et al., 2003). Luna et al. (2005), exploring the effect of the life history on genetic structure of two *Chamaedorea* species, found less genetic divergence for the abundant wind-pollinated understory palm *C. tepejilote* than for the scarce entomophilous climbing palm *C. elatior*. Moderate genetic structure for the dioecious palm *C. ernesti-augusti* has been reported in Belize (Cibrián-Jaramillo et al., 2009).

Conclusions and Directions for Future Work

Current knowledge on palm resilience in relation to anthopogenic disturbances in tropical America remains relatively scarce, and mainly focused on the effects of two disturbance drivers: habitat fragmentation and harvest (Fig. 4). Several palm-rich regions of South America are especially understudied (the north-western Pacific coast, the Andes, the northern part of the South Cone).

Common methodological approaches, such as the use of transition matrices (see Pinard & Putz, 1992), and the setting of removal experiments, contribute to give strength to the available data and allow for meaningful comparisons. These studies have direct applications for management practices, providing quantitative estimates of turnover and intensity of extraction for sustainable use of the target species. However, a more generalized use of permanent plots and long-term studies is needed, since extrapolation based on short-term studies is uncertain for slow-growing palms. Permanent plots set near rain forest research stations are an extremely valuable resource (Yasuni, Ecuador, e.g. Vormisto et al., 2004; La Selva, Costa-Rica, e.g. Sezen et al., 2007; Norden et al., 2009; El Cielo, Mexico, Endress et

al., 2004b; Los Tuxtlas, Mexico, Martínez-Ramos et al., 1988; Barro Colorado island, Panama, e.g., Wright & Duber, 2001) that could be more intensively used for this purpose, inclusively by analyzing more throughoutly existing data.

Despite a relatively high number of studies on palm resilience, this review highlighted a lack of integration of the results obtained into the ecological conceptual framework (Fig. 4), with discussions focused on conservation and on rehabilitation of degraded ecosystems. An interesting attempt of integration was that of Orellana (1992), who proposed a classification of palm resilience based on the C-S-R strategies of Grime (1979). In order to progress in this direction, the development of a mechanistic approach is required in future research, that should explore various disturbance types taking more into account the following aspects:

- Microenvironmental information, including analysis of alteration of soil composition, moisture and microclimate.
- Species traits (morphological, physiological, reproductive), and their variation under disturbance
- Palm communities, for direct comparisons among species
- Representativeness of palm floras and ecosystems, unbiaised by socio-economic considerations or conservation concern, in order to gain a more general overview of resilience patterns in palms.

Under these conditions, data on the resilience of tropical American palms may be used consistently to discuss crucial ecological concepts such as the intermediate disturbance hypothesis, which is understudied in the tropics (Bongers et al., 2009), and the role of plant-plant interactions, suggested to have a positive impact on ecosystem resilience in humid tropical environments (Gomez-Aparicio, 2009), although more commonly described in highly constrained environments so far (stress gradient hypothesis; see Brooker et al., 2008 for a review).

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