

# PLANT COMMUNITY STRUCTURE AND FUNCTION IN A SWAMP FOREST WITHIN THE ATLANTIC RAIN FOREST COMPLEX: A SYNTHESIS

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## ABSTRACT

(Plant community structure and function in a swamp forest within the Atlantic rain forest complex: a synthesis) This paper synthesises a decade of research on a swamp forest within the Atlantic forest complex in the state of Rio de Janeiro, Brazil. I propose that this swamp is a fragile ecosystem, since its diversity and functioning are highly dependent on a specific interaction between two functional groups: shade-providers (locally rare trees) and providers of safe germination sites (terrestrial bromeliads). This conclusion is based on a broad set of data regarding plant ecophysiology, population and community ecology and phytogeography, which I review here. I discuss the implications of these findings for conservation and restoration of swamps at the Atlantic forest complex.

**Key-words:** clonal growth, epiphytes, functional groups, photosynthesis, swamp forest.

## RESUMO

(Estrutura e funcionamento da comunidade vegetal de um pântano no domínio do complexo da floresta pluvial atlântica: uma síntese) Este artigo sintetiza uma década de pesquisas realizadas em um pântano pertencente ao complexo vegetacional atlântico no estado do Rio de Janeiro, Brasil. Eu proponho que este pântano é um ecossistema frágil, na medida em que seu funcionamento e sua diversidade são altamente dependentes da interação específica entre dois grupos funcionais: os geradores de sombra (árvores localmente raras) e os geradores de sítios seguros para germinação (bromélias terrestres). Esta conclusão se baseia num amplo conjunto de dados referentes à ecofisiologia, ecologia de populações e comunidades, e fitogeografia, que são revisados aqui. Eu discuto as implicações destes resultados para a conservação e restauração deste tipo de vegetação.

**Palavras-chave:** crescimento clonal, epífitas, estabilidade de ecossistemas, fotossíntese, grupos funcionais, pântano.

## INTRODUCTION

Although Brazilian flooded habitats represent a considerable proportion of the continent's (and therefore of the world's) wetlands, the major wetlands of Brazil cover only 2% of the country's large territory (WCMC 1992). This may partly explain why, from a plant ecology standpoint, Brazilian freshwater wetlands are still less than well known. Despite some relevant scientific efforts regarding Amazonian flooded forests (e.g., Parolin *et al.* 2004), the Pantanal Matogrossense (e.g., Pott 2000), and the gallery forests of central and southeastern Brazil (e.g., Lobo & Joly 1998), there are still many gaps to be filled. For instance, hardly any scientific concern has been directed towards the freshwater swamp forests of the Atlantic forest complex in south-eastern Brazil, and their existence is not even mentioned in

reviews of Brazilian (Joly 1990) and South American (Junk 1993) wetlands. Perhaps, this is because very little of the once extensive Atlantic rain forest (ARF) remains intact and its lowlands, especially, have been severely impacted. Estimates of deforestation of the ARF are always alarmingly high, ranging from 90 to 98% (e.g., Leitão-Filho 1993; Myers *et al.* 2000; WCMC 1992).

Nevertheless, the ARF stands out as one of the main centres of biodiversity in the world, with high species diversity and high levels of endemism. It is considered one of the 25 biodiversity hotspots of the world for conservation priority (Myers *et al.* 2000). However, it is often unclear what is considered as ARF, which results in some of the variation regarding the deforestation estimates above. For instance, in recent review papers, Morellato & Haddad (2000) defined it as a vegetation

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composed of a coastal rain forest and a semi-deciduous forest type; Oliveira-Filho & Fontes (2000) proposed a more comprehensive definition encompassing rain forests, semi-deciduous forests and also the southern subtropical *Araucaria* forests and the north-eastern enclaves of *brejo* forests; and Scarano (2002), following Rizzini (1979), was even broader and proposed that from evolutionary and conservation viewpoints the Atlantic coastal vegetation of Brazil, particularly in the case of the State of Rio de Janeiro, should be treated as a mosaic comprising all forest types (including swamps and mangroves) and also the neighbouring open vegetation (such as those on *restingas* and *inselbergs*).

In this paper we follow the perspective of Rizzini (1979) and Scarano (2002), while reviewing a decade of research in one of the vegetation types at the periphery of the ARF *sensu stricto*, i.e. the lowland swamp forests. The plant communities at the periphery of the ARF (see Scarano 2002) are subjected to more extreme environmental conditions than those in the mesic rain forest (Scarano *et al.* 2001), but their flora often consists mostly of rain forest species (Rizzini 1979). These marginal communities are faced with a wide array of adverse environmental conditions, such as high and low temperatures including freezing, flooding, drought, constant wind, high salinity and lack of nutrients. Thus, diversity, productivity and structural complexity are expected to be lower in these communities.

The studies reviewed here were conducted in one of the last well-preserved remnants of swamp forest in the Biological Reserve of Poço das Antas, state of Rio de Janeiro. At this point, it is important to highlight that the Portuguese word for swamp – ‘*pântano*’ – is hardly ever used in Brazil to describe “*forested freshwater wetlands on waterlogged or inundated soils ...*”, as quoted from the Ramsar Convention that attempts to define wetlands (WCMC 1992). Dorneles & Waechter (2004) lists a series of terms used to describe Brazilian forests

subjected to phreatic flooding and ‘*matinha pantanosa*’ is the closest it gets to swamp. Although it is clear that the classification of the Ramsar Convention is fraught with problems, due to the enormous variety of wetland types even within a given group (see WCMC 1992) such as ‘swamp’, in Brazil there should be an attempt to standardize the terminology of such forests.

The hypothesis first forwarded by Scarano *et al.* (1998), to explain the low resilience of the swamp forests of Poço das Antas, is now further developed, and I present a more detailed functional model describing interactions between distinct plant functional groups. Finally, I discuss the relevance of these findings for conservation and restoration of these wetlands, as well as some of major research gaps to be filled regarding the ecology of Atlantic forest swamps.

## STUDY SITE

The data reviewed here were collected inside ca. 2 ha of a well-preserved remnant of swamp forest in the Biological Reserve of Poço das Antas (22°30’S, 42°15’W), municipality of Silva Jardim, state of Rio de Janeiro, south-east Brazil. The Reserve covers *c.* 5000 ha with a perimeter of 44 km. Rainfall is well distributed throughout the year, with a discrete dry season from May to August. Plants growing in the swamp forests withstand *c.* 100–365 d per year of phreatic flooding, depending on topographic position. This forest remnant shows a topographic gradient from a flood-free site through a periodically flooded site to a permanently flooded site. Scarano *et al.* (1997) described the differences between the periodically and the permanently flooded sites. The terrain of the periodically flooded site is slightly irregular due to subtle topographic variations. The local differences between lower and higher patches are often < 30 cm, but this is sufficient to cause large differences in terms of the duration of flooding. The lower patches are likely to be flooded for up to 300 d per year, while the higher patches may be entirely

free of flooding in certain years. Thus, there is a mosaic of flooded and non-flooded patches which will unpredictably vary throughout the year depending upon the rainfall. The permanently flooded site differs for having a superficial water-table reaching up to 30 cm deep, and a more open canopy. These differences result in distinct floristic compositions: while the periodically flooded site has higher species diversity, the permanently flooded site is a monodominant forest, where the deciduous tree *Tabebuia cassinoides* (authorities and families of plant species are listed in Table 1, unless otherwise stated) contributes with some 63% of the adult trees and the herb stratum is densely occupied by bromeliads.

These swamps were subjected in a recent past (ca. 40 years) to wood extraction and changes in the flood-regime due to the construction of a dam. Forest fragments rise from large extensions of treeless peat which, at one time, were swamp forests. The virtual disappearance of these once large extensions of forest resulted in the fragmentation of flood-free forests and, among many other consequences, in the almost extinction of the golden-lion-tamarin (*Leontopithecus rosalia rosalia*) which has a preference for this habitat. The extent of this damage is such that the Reserve, which was created to preserve the last specimens of this animal, has 40% of its total area either partially or totally degraded (IBDF 1981).

**Table 1** - Species abundance in a 0.5 hectare plot in the permanently flooded swamp. Plants sampled had diameter at breast height  $\geq 3.5$  cm.

Species (Family)	No. of trees	Classification
<i>Tabebuia cassinoides</i> DC. (Bignoniaceae)	1110	Monodominant
<i>Calophyllum brasiliense</i> Camb. (Clusiaceae)	83	Abundant
<i>Symphonia globulifera</i> L. (Clusiaceae)	69	
Myrtaceae sp.	69	
Melastomataceae sp.	52	
<i>Lonchocarpus cultratus</i> (Vell.) Az. Tozzi & H.C. Lima (Fabaceae)	50	
<i>Myrcia racemosa</i> (O. Berg) Kiaersk (Myrtaceae), <i>Henriettea</i> sp. (Melastomataceae), <i>Euterpe edulis</i> Mart. (Arecaceae), <i>Eugenia expansa</i> Spring (Myrtaceae), <i>Tabebuia umbellata</i> (Sond.) Sandwith (Bignoniaceae), <i>Eugenia cachoeirensis</i> Berg (Myrtaceae), <i>Andira fraxinifolia</i> Benth. (Fabaceae), plus four more species	11<n<33	Intermediate
<i>Eugenia umbosa</i> Berg (Myrtaceae), <i>Myrcia fallax</i> (Richard) DC. (Myrtaceae), <i>Platymiscium floribundum</i> Vogel (Fabaceae), <i>Tovomitopsis paniculata</i> Planch & Triana (Clusiaceae), <i>Bredemeiera autranii</i> Chod. (Polygalaceae), <i>Gomidesia sellowiana</i> O. Berg (Myrtaceae), <i>Bactris</i> sp. (Arecaceae), <i>Marlierea georgeana</i> G.M. Barroso (Myrtaceae), <i>Sparattosperma leucanthum</i> (Vell.) K. Schum. (Bignoniaceae), <i>Inga edulis</i> (Vell.) Mart. ex Benth. (Mimosaceae), <i>Alchornea triplinervia</i> Muell. Arg. (Euphorbiaceae), <i>Brosimum guianensis</i> (Aubl.) Huber, <i>Eriotheca pentaphylla</i> (Vell.) A. Robyns, <i>Trichilia</i> <i>martiana</i> C. DC. (Meliaceae), plus 28 more species.	< 10	Rare
<b>TOTAL: 59 species</b>	<b>1744 trees</b>	

## RELEVANT TRAITS OF SPECIES AND POPULATIONS

The fact that the Biological Reserve was created in 1975, and up to this day there are hardly any signs of natural regeneration in the deforested areas, points out for the low resilience of these swamp forests. Resilience is the return time to functional processes existing prior to perturbation (Pimm 1991; Shrader-Frechette & McCoy 1993), thus it is a measure of time for recovery (but see Gunderson, 2000). Since functional processes and interactions are largely unknown for tropical rain forests in general, particularly in the long-term, it becomes very difficult to assess the resilience of a given plant community (Ives 1995). Before I introduce the "low resilience hypothesis" forwarded by Scarano *et al.* (1998), it is necessary to describe some relevant characteristics of plant species and populations at this site. These traits refer to plant regeneration, establishment and maintenance.

### Flood-resistance: tolerance or avoidance

Aerobic organisms, such as higher plants, need an adequate supply of oxygen for the performance of vital functions, such as cell division. However, plants and animals are capable to survive under partial or total lack of oxygen, and there is a large interspecific variation regarding the length of time they can do so (Hendry & Crawford 1994). In the case of higher plants, survival under oxygen shortage can last from hours to years (Crawford 1992). Flooding induces oxygen shortage in the soil, which directly affects the roots of plants. Thus, in order to colonize a flood-prone habitat, plants must resort to biochemical, physiological and/or morpho-anatomic mechanisms to tolerate or avoid the deleterious effects of oxygen deprivation. Even possessing such mechanisms, these individuals must overcome dispersal, germination and young age hazards.

Variation in flooding resistance means distinct patterns of spatial distribution and abundance for each species, which will result

in different community structures. For instance, Table 1 presents some original data regarding species composition and abundance in 0.5-hectare of the permanently flooded swamp. Many of the species listed as intermediate or rare in local abundance are actually more conspicuous in the contiguous periodically flooded forest (see Guedes-Bruni *et al.* 2006) or even on the flood-free hills. Perhaps the most notable example of resistance to flooding is *Tabebuia umbellata*, which has an intermediate abundance in the permanently flooded swamp. It is a typical flood-tolerant plant that showed radial growth in the stem during long-term flooding (Callado *et al.* 2004). Very few tree species in nature display growth increment while flooded and *T. umbellata* can be ranked among plants such as *Taxodium distichum* (L.) Rich. (Taxodiaceae), *Nyssa aquatica* L. (Nyssaceae), some species of *Salix* and the mangroves (Kozłowski 1984). The deciduous, monodominant *Tabebuia cassinoides* showed, instead, leaf fall and cambial dormancy during permanent flooding (Callado *et al.* 2001a, b). This also appears to be an efficient survival strategy given the high abundance of this species.

### Germination and establishment

However, before this myriad of tolerance and avoidance mechanisms can be triggered, plant species still have a major hurdle to overcome: the germination and establishment phase. Scarano *et al.* (1997) produced a detailed account of distinct establishment strategies taking place in both periodically and permanently flooded swamps. We argued that the swamp forest showed a spatial and temporal heterogeneity which guaranteed the existence of some permanent or transient safe (non-flooded) germination sites at any given moment. Spatial heterogeneity was the result of non-flooded patches in the periodically flooded zone and of tank-bromeliads in the permanently flooded zone. Although habitat patchiness and unpredictability are likely to cause difficulties to the optimization of phenological timing (Colwell 1974; Rees 1994),

seed reproduction stands a better chance of taking place at such sites rather than in a uniformly inhospitable habitat (see Cook 1980). Thus, germinating seeds and young seedlings were found in flood-free soil patches and also inside the tanks of bromeliads that densely covered the understory of the permanently flooded zone. For instance, in the periodically flooded site, *Tovomitopsis paniculata* was more frequent in non-flooded than in flooded soil patches. However, vegetative propagation appeared to play a role in the colonization of flooded patches, where seeds of this species sink and rapidly lose viability. In the permanently flooded site, seedlings of the two *Tabebuia* species (*T. cassinoides* and *T. umbellata*) were found in large numbers on litter trapped by tanks of understory bromeliads, which provide a safer germination site than the stagnant flood-water below them. The gradual death and fall of external leaves of the bromeliad rosettes may favour fixation of seedlings growing in lateral tanks on the swampy ground, thus constituting a key factor in the success of seed propagation in this vegetation. Evidences of bromeliads facilitating seed germination of woody plants were later found also in the restingas, another habitat at the periphery of the Atlantic forest (Scarano 2002).

Another interesting example of successful seed establishment is that of the locally abundant, flooding specialist, *Calophyllum brasiliense*. Scarano *et al.* (1997) found that seed-originated juveniles of this species were as frequent in flooded as in non-flooded patches and showed a reversed-J frequency distribution of individuals per height class in the periodically flooded site. Two types of seed dormancy (one imposed by the fruit pericarp and another which manifested itself even in the absence of the pericarp) and a two-phase (bat and water) dispersal syndrome played a key role in this pattern. These features resulted in different timing of germination among seeds of a same cohort, which is most likely suitable to the variability and uncertainty of their habitat.

### Vegetative reproduction and clonal growth

Abrahamson (1980) argues that in extreme habitats a combination of sexual and asexual reproduction should give a plant optimal fitness. However, to some extent, the examples of *T. paniculata* and *C. brasiliense* seem to be trade-offs between success of seed vs. vegetative reproduction in this swamp. The seeds of the former rapidly rot in the lower-lying patches where flooding lasts longer, and this species colonises these patches mostly by vegetatively originating regenerants; the seeds of the latter seem to be highly adapted to flooding and the species does not reproduce vegetatively. *Symphonia globulifera*, nevertheless, seems to combine vegetative propagation with seed/seedling adaptation to flooding: it occurred indistinctly in flooded and non-flooded patches and there was no significant preference by the vegetatively formed regenerants for any patch type. Seed buoyancy was observed in the field and may be one of the factors accounting for this pattern. *T. cassinoides*, similarly, may combine both strategies, with pronounced asexual reproduction via roots and fallen trunks and seed germination and establishment within bromeliad tanks (Scarano *et al.* 1997; 1998).

There are many limitations to the direct investigation of clonal growth patterns in trees (but see Cirne & Scarano 2001), particularly in swamps. On the other hand, we did collect some data regarding clonal growth of bromeliads (Freitas *et al.* 1998; 2003), given their dense cover of the understory and their importance as safe germination sites to other plant species. We found clear habitat segregation between two closely related species of *Nidularium*, *N. procerum* Lindm. and *N. innocentii* Lem. Both species showed estimates of more than 40,000 rosettes per hectare, which we attributed mostly to clonal propagation given that we found no evidence of bromeliad establishment via seed germination during five years of observation. While *N. procerum* densely occupied permanently flooded, semi-exposed ground, *N.*

*innocentii* preferably occupied the periodically flooded, deep-shaded zone. Interestingly, there was a narrow boundary zone where, although ramets of both species neither overlap nor intermingle, one species occupied the habitat seemingly preferred by the other. This allowed us to compare parameters related to population structure and leaf morphology and structure. We expected that both species would have a smaller ramet density per square meter at the non-preferred habitat as compared to the preferred one, and also that they would not show morpho-structural plastic variation in response to the non-preferred. This expectation derived from the hypothesis that segregation would be due to poor adaptation of each species to the other species preferred site. The fact that there was no site-related density variation to either species and that morpho-structural variation occurred in both for 4-5 parameters typically related to light/shade acclimation, suggested that they were both acclimated to each other's preferred habitat. This suggested that habitat segregation between these two species was neither directly related to flooding nor to light regime (Freitas *et al.* 2003).

This conclusion contradicted what we had previously forwarded in Scarano *et al.* (1999): we then proposed that segregation between these two species was due to ecophysiological differences regarding light-use. *N. procerum* is an obligate CAM plant (crassulacean acid metabolism), which occurred predominantly under the more open canopy of the permanently flooded site, whereas *N. innocentii* is a  $C_3$  plant, which occurred predominantly in the shadier understorey of the periodically flooded site. It was, however, clarified in Freitas *et al.* (2003) that although *N. innocentii* has physiological and morphological features more typical of shade plants than the CAM species *N. procerum*, the latter could be successful in the deeply shaded, intermittently flooded site occupied by the population of *N. innocentii* and vice-versa. Thus, we then proposed that both species could adapt to the light/flooding

regimes found in the understorey of the swamp forest, and segregation was then due to colonization history (e.g., timing of arrival and establishment) at the site and subsequent competition for space and exclusion. Colonization may have occurred during a single or few events in the past when the proper environmental conditions existed for establishment of seedlings on the forest floor (e.g., a prolonged dry period) followed by pronounced clonal growth in subsequent years. The dense, clonal colonies of the rosettes of both species now act as a physical barrier to the establishment of the other species.

Since both plants are typically epiphytes in the coastal rain forest, we attributed their unlikely occurrence as flooded, terrestrial plants to the fact that they could root more easily on a horizontal surface, maintain greater stability for their rosettes, experience less competition on the flooded floor of the swamp forest, and more obviously, their rhizomes were flood-tolerant. We described them as "epiphytes on mud" (Freitas *et al.* 1998, 2003; Scarano *et al.* 1999).

## COMMUNITY STRUCTURE

The vegetation structure of this swamp forest varies from the periodically flooded site to the contiguous permanently flooded site. The periodically flooded site was surveyed by Guedes-Bruni *et al.* (2006) and showed higher species richness ( $S=97$ ) and diversity, as assessed by the Shannon-Wiener index ( $H'=3.98$ ), than the permanently flooded site ( $S=59$  and  $H'=1.30$  respectively; see Scarano *et al.* 1998 and Table 1). Although sampled area (1 ha vs. 0.5 ha respectively) and the selection criteria for sampling (diameter at breast height  $\geq 10$  cm vs. 3.5 cm respectively) differed, the permanently flooded site is markedly less diverse than the periodically flooded site. As discussed before, this was due to the marked dominance of *Tabebuia cassinoides* that accounted for ca. 63% (1110 out of 1744) of the trees. Indeed, Dorneles & Waechter (2004) reviewed a number of papers

about Brazilian swamps of different parts of the country and claimed that they often have low diversity due to the dominance of only a few species. The longer periods of flooding that plants are exposed to in this site may account for this reduced diversity in the permanently flooded site. The species richness on this site is however high as compared to other Brazilian swamps (see Dorneles & Waechter 2004 and references therein) which, on the other hand, may be due to ecological plasticity of habitat generalists (most of the locally rare species; Table 1) and to the creation of flood-free germination sites by bromeliad rosettes.

The other important structural component is the understorey, which, as we have seen, is densely covered by bromeliads. This dense cover is particularly evident in the permanently flooded zone that, in addition to having a monodominant overstorey (*T. cassinoides*), has also a monodominant understorey (*N. procerum*). In the periodically flooded zone the understorey is less dense and in addition to *N. innocentii* other bromeliads are found in separate colonies, such as *Quesnelia quesneliana* (Brong.) L.B. Smith. Bromeliads, particularly in the permanently flooded site, play a key ecological role creating safe germination sites, as seen above. Then, we were interested in determining which were limiting factors for the life of the bromeliads. Scarano *et al.* (1999) showed that both *Nidularium* species are intolerant to full sunlight. We even classified *N. procerum* as a shade-adapted CAM plant. Thus, if the creation of safe germination sites is a key ecological role, the generation of shade, needed by these "live germination sites", is also relevant.

### THE LOW RESILIENCE HYPOTHESIS

Scarano *et al.* (1998) compared the number of tree species spontaneously re-established at three different Brazilian vegetation types 10 years after anthropogenic perturbation: an *igapó* forest in the Amazon, a low montane Atlantic rain forest in the Brazilian south-east, and the swamp forests of this Reserve. We found out that while the former two reached

species richness values similar to those presented prior to perturbation, the latter showed no recovery at all. We then forwarded a hypothesis to explain the low resilience of these swamps, based solely on some of the results described above for the permanently flooded site. We proposed that two functional groups of plants played vital ecosystem functions regarding the maintenance of diversity: a) germination site-providers (a role played by bromeliad species, and particularly *N. procerum*); and b) shade-providers (a role played by evergreen trees, which were mostly found among the groups with intermediate or rare abundance shown in Table 1. It is important to note that they create a semi-shade regime, and not a deep shade one, as described previously). A third functional group would be formed by the monodominant *T. cassinoides*, which can establish and grow irrespective of safe germination site or shade, given its pronounced resistance to flooding, full sun-light and asexual reproduction. Moreover, this is a deciduous tree that remains leafless for 3-4 months per year (Callado *et al.* 2001b). Thus, it does not fit in b), the group of shade-providers. We hypothesized that removal of the shade-providing, locally rare trees would result in the disappearance of bromeliads and *vice-versa*, whereas *T. cassinoides* population would remain unaffected.

The low resilience of this swamp vegetation, and its consequent inability to recover after impact, is possibly due to the permanent change in the soil water regime caused by past damming of rivers, which for several areas implicated on either drainage or deeper and longer flooding than usual. This may have resulted in removal of the tree cover, which in turn might have exposed bromeliads to direct sunlight and death in the medium-term. Thus, tree removal could mean bromeliad death and, as a consequence, no seed regeneration. If this tree-herb mutualism is true, this complex interaction could provide the basis upon which this ecosystem develops. It is worth mentioning that tree regeneration could still be possible through asexual reproduction commonly seen in these sites, but then diversity would be even

lower than in undisturbed forests. Furthermore, swamp degradation gave way locally to treeless turf, which is highly flammable; fire events are all too common on these locations, and consist of additional impediment to natural recovery.

If this hypothesis is at all confirmed in the future, it would appear that low resilience, and thus low stability, could be associated to reduced species diversity as that found in the permanently flooded swamp forest. There has been much controversy around the relationship between diversity and stability (see reviews in Scarano *et al.* 1998; Scarano & Dias 2004), which is mostly due to the difficulties in measuring important components such as those related to interactions between species and complexity. The functional group approach, as seen above, reduces complexity and helps formulate testable hypotheses about the role of given species in the ecosystem and, in this respect, detect ecological redundancies and singularities of these species (Díaz *et al.* 2003; Smith *et al.* 1997; Wilson 1999). Current advances in mathematical tools to investigate such ecological groupings, particularly in Brazil (Pillar 1999; Pillar & Sosinski 2003), can promote a fast progress of this research line.

#### LESSONS IN THEORY AND APPLICATION

The distinction between theoretical and applied ecology is often misleading, and it may not actually exist at the frontiers between Ecology – Conservation – Restoration. The stability concept and the need to measure it as an ecological parameter (see Tilman *et al.* 2001) is as relevant to “pure research” - as some authors would like to classify it - as it is to achieve more applied goals regarding conservation and ecological restoration. Similarly, answers to questions such as “what is the ecosystem effect of the loss of one species?”, or “how does species diversity relate to stability?” are as relevant to a theoretical ecologist as they are to a decision-maker (see Barbosa *et al.* 2004). Thus, a formal test of the pertinence of the functional groups proposed in the “low resilience hypothesis”, as discussed above, could generate important by-products to conservation and restoration.

This first decade of studies in the swamp forests of Poço das Antas is clearly only the beginning of a long-term research programme. However, even at an early stage, this case study has potential to provide fuel for a number of theoretical debates. For instance, the data produced in these studies address at least two hot theoretical topics in Ecology: a) the need to integrate facilitation (e.g., Bruno *et al.* 2003; Callaway *et al.* 2002) and competition (e.g. Fargione & Tilman 2002; Grime 2001) models to improve niche theories (i.e., those that examine the role of interactions between species in ecosystem properties such as stability and productivity – see also Chase & Leibold 2003); and b) the need to integrate these niche theories with the so-called neutral theories (i.e., those that examine the relationships of species richness and/or diversity with ecosystem properties – they are called neutral for assuming the premise that interactions do not explain large scale ecosystem processes, such as in Hubbell 2001; MacArthur & Wilson 1967). Scarano & Dias (2004) have recently argued that such dualisms exist due to the fact that these distinct types of theories were produced in very different ecosystems: while niche models and theories have often been produced in habitats with low species diversity and low resource availability, neutral theories have frequently emerged from habitats with higher species richness and resource availability. The swamp forests of Poço das Antas have an unusual combination of high species richness and low resource (i.e., soil oxygen) availability. Future studies and experiments on resilience and stability and their relationship with species interactions (niche perspective) and dispersal processes within a biogeographical framework (neutral perspective) may prove fruitful and challenging to ongoing theoretical thought in Ecology.

Locally, our studies seem to indicate that restoration of lands previously occupied by swamp forests will require much human effort and intervention. A forest cover in the lowland areas, now occupied by treeless turf, would be essential to create corridors linking forest fragments and increasing the habitat range of a

number of animal species, such as the threatened golden-lion-tamarin. Frequent fires on the turf seem to impair natural recolonisation by tree species and, moreover, changes in the soil hydrology of such sites may not allow the reconstitution of swamps. Thus, fire control allied to the development of restoration techniques on a turf substrate are recommendations that emerge from our studies. The successful experience with forest restoration of non-flooded soils, described by Moraes & Pereira (2003), is strong evidence that reforestation of the turf cover and the enhancement of connectivity between forest fragments (see also Metzger 2003) may soon be triggered.

On the other hand, can we apply the model proposed here to describe structure and function of other Brazilian swamps or the patterns and processes described are strictly local? This question cannot be answered at present, since this vegetation type has not been thoroughly surveyed in the country. Furthermore, the wealth of regional terminologies attributed to forests subjected to phreatic flooding suggests both that a large variety of forest types should be expected, and also that more comparative and integrative work is required to compare such forests as regards to floristics, ecology and biogeography.

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