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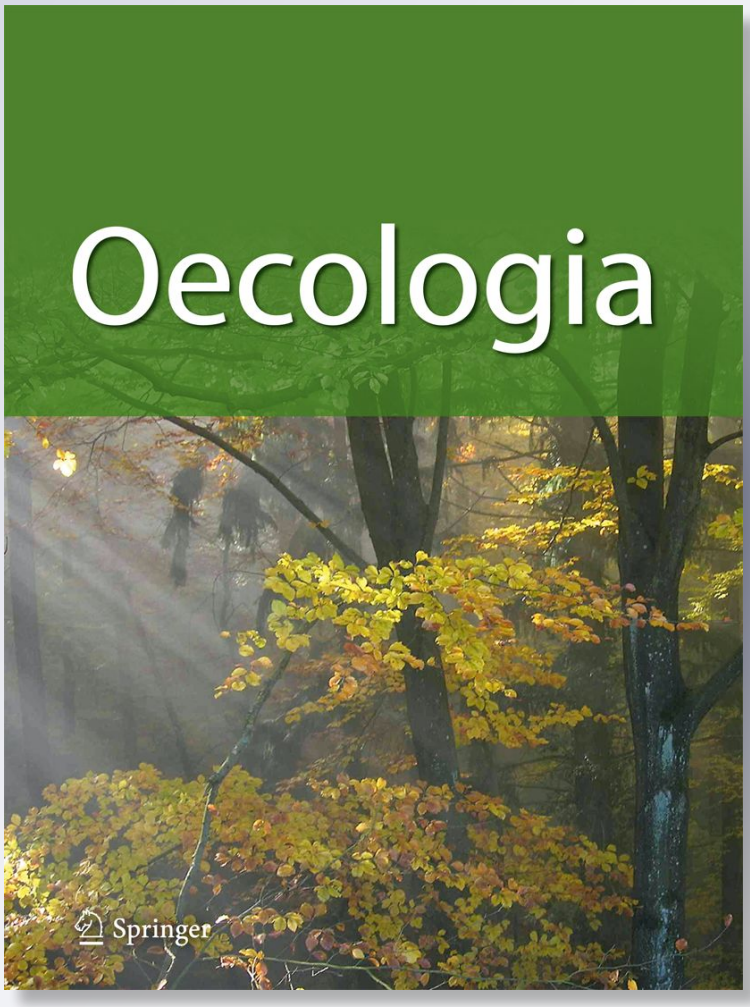
Oecologia

ISSN 0029-8549

Oecologia
DOI 10.1007/s00442-011-2100-3



Springer

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PHYSIOLOGICAL ECOLOGY - ORIGINAL PAPER

Diaspore bank of bryophytes in tropical rain forests: the importance of breeding system, phylum and microhabitat

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Received: 27 January 2011 / Accepted: 26 July 2011

Abstract Diaspore banks are crucial for the maintenance and resilience of plant communities, but diaspore banks of bryophytes remain poorly known, especially from tropical ecosystems. This is the first study to focus on the role of diaspore banks of bryophytes in tropical rain forests. Our aim was to test whether microhabitat (substrate type) and species traits (breeding system, phylum) are important in explaining the diaspore bank composition. Using samples cultivated in the laboratory, we assessed the number of species and shoots emerging from bark, decaying wood and soil from two sites of the Atlantic rain forest (montane and sea level) in Brazil by comparing the contribution of species by phylum (mosses, liverworts) and breeding system (monoicous, dioicous). More species emerged from bark (68) and decaying wood (55) than from soil (22). Similar numbers of species were found at both sites. Mosses were more numerous in terms of number of species and shoots, and monoicous species dominated over dioicous species. Substrate pH had only weak effects on shoot emergence. Species commonly producing sporophytes and gemmae had a high contribution to the diaspore banks. These superficial diaspore banks represented the extant vegetation rather well, but held more monoicous species (probably short-lived species) compared to dioicous ones. We propose that diaspore bank dynamics are driven by species traits and microhabitat characteristics, and that short-term diaspore banks of bryophytes in tropical rain forests contribute to fast (re)establishment of species after disturbances and during succession, particularly dioicous mosses investing in asexual reproduction and monoicous mosses investing in sexual reproduction.

Keywords Asexual diaspores · Establishment · Liverworts · Mosses · Spores

Introduction

Diaspore banks are important for maintenance of genetic variability and resilience of plant communities, mainly in ecosystems having an unfavorable dry or cold season (Thompson 2000). Seed banks have been widely studied in different ecosystems mainly to determine which habitat or species characteristics affect the seed-bank composition. Compared to seed banks, diaspore banks of bryophytes remain little understood, although there are some surveys from temperate and boreal areas (Jonsson 1993; Bisang 1995; During 1997; Sundberg and Rydin 2000) and a few studies from tropical ecosystems (During 1997, 2007; Bisang et al. 2003; Maciel da Silva and Lins-Silva 2007). Bryophyte diaspore banks differ from seed banks in two basic ways. First, in addition to spores they may contain a large diversity of asexual diaspores, such as gemmae, caducous leaves and buds, and bryophyte fragments capable of regenerating. Second, they have a large number of big

Communicated by Allan Green.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-2100-3) contains supplementary material, which is available to authorized users.

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Published online: 13 August 2011

spores and asexual diaspores, since small spores tend to be long-range dispersed and seem more short-lived than large spores (Jonsson 1993; During 1997; Löbel and Rydin 2010).

There is a considerable variation in life histories among bryophytes which are characterized by different reproductive trade-offs (During 1979). In general, monoicous species produce spores more frequently than dioicous ones (Longton 1992). Species, particularly liverworts, that fail to produce spores are generally rare (Laaka-Lindberg et al. 2000). Bryophytes thus offer interesting models to investigate the influence of breeding systems (monoicous, dioicous and polyoicous), diaspore types (spores, gemmae, fragments), phylum (mosses, liverworts and hornworts) and habitat features on the dispersal and establishment processes.

Although little is known about the role and function of bryophyte diaspore banks in tropical rain forests, bryophytes are a large and important component in these forests, contributing to not only the high species richness and diversity (Frahm and Gradstein 1991) but also to these ecosystems' functionality (nutrient and water cycling, microfauna habitat; Schofield 1985; Turetsky 2003). Tropical rain forests are extremely threatened, especially in the countries undergoing rapid economical development. For example, the Atlantic forest in Brazil now has <7% of its original cover (Tabarelli et al. 2005) and is restricted to small forest fragments and a few large nature reserves. Despite the intense deforestation, the Brazilian Atlantic forest retains a high number of plant species, with a total of 15,782 (7,155 endemic species), of which 1,230 are bryophytes (Stehmann et al. 2009).

Our general aim was to test whether microhabitat characteristics, such as substrate type, and species traits (breeding system and phylum), are important to the pattern of bryophyte diaspore banks in tropical rain forests. Specifically, we compared the emergence (species occurrence and shoot abundance) of mosses and liverworts, differing by breeding system (monoicous, dioicous and polyoicous), from the main substrates (decaying wood, bark, soil) in two sites in order to cover the range of environmental variation of the Brazilian Atlantic Ombrophilous Dense Forest (montane and sea level forests; see Alves et al. 2010), over two seasons (dry and rainy). Our hypotheses were:

(1) The diaspore bank should be dominated by monoicous species, since they produce sporophytes more frequently than dioicous ones (Longton 1992; Oliveira and Pôrto 1998).
(2) There should be more mosses than liverworts in the diaspore bank, since the richness of mosses in the Brazilian Atlantic forests is generally higher than that of liverworts (Costa 2009). However, we expected more liverworts at sea level than at the montane site, because liverwort richness tends to be higher in lowland tropical forests (Cornelissen and Gradstein 1990; Costa 1999; Visnadi 2005).
(3) The number of species in the diaspore bank should be lower in soil than in decaying wood and bark, reflecting the richness typically found in these substrates in tropical rain forests (Visnadi 2005; Santos and Costa 2008). In addition, we expected that the substrate pH should have different effects on the establishment of mosses and liverworts with different breeding systems (Löbel and Rydin 2009, 2010).
(4) We expected more species in the diaspore bank in samples collected in the dry season when more species have a peak in spore dispersal (Pôrto and Oliveira 2002; Maciel-Silva, unpublished data).

Materials and methods

Study sites

The field sites selected for this study were located within a larger project dealing with floristic composition, structure and functioning of the Serra do Mar State Park (Alves et al. 2010). This park is covered by a tropical rain forest, referred to as the Atlantic Ombrophilous Dense Forest (Veloso et al. 1991), which is characterized by temperatures of around 25°C and heavy precipitation distributed fairly regularly over the year. The study sites were situated in the Núcleo Picinguaba (23°31′–23°34′S, 45°02′–45°05′W) and in the Núcleo Santa Virgínia (23°17′–23°24′S, 45°03′–45°11′W) of the Serra do Mar State Park, São Paulo State, Brazil (Veloso et al. 1991). The Núcleo Santa Virgínia has approximately 5,000 ha of forest, from 850 to 1,100 m a.s.l., and the Núcleo Picinguaba has approximately 47,500 ha of forest, from sea level to 1,340 m a.s.l.

The study sites were chosen to represent the extremes of an altitudinal and floristic variation of the Atlantic Ombrophilous Dense Forest (see Alves et al. 2010). The low altitude forest is locally known as a *restinga* forest, i.e., close to the sea and seasonally flooded, and is referred to here as our sea-level site (N. Picinguaba), while the high-altitude site (about 1,000 m a.s.l.) is called a montane forest (N. Sta. Virgínia). The montane soil is rich sand/clay, while the sea-level site has nutrient-poor sand. The total biomass is higher in the montane forest than at sealevel (Alves et al. 2010). The two sites are about 35 km apart.

Minimum and maximum temperatures, relative air humidity, PAR (photosyntetically active radiation from 400 to 700 nm) and the red:far-red ratio (650:730 nm) in the understory at both sites were measured monthly or

Table 1 Microclimatic parameters measured at the montane and sea-level sites, August 2007 to May 2009

Values are medians with upper and lower quartiles for light measurement, and mean ± standard deviation for humidity and temperature

Parameters	Montane	Sea level
PAR (μmol m^{-2} s^{-1}); sunfleck	140 (39–448, n = 12)	712 (198–1,035, n = 8)
Red:Far red ratio; sunfleck	1.0 (0.69–1.11, n = 12)	1.2 (0.80–1.40, n = 6)
PAR (μmol m^{-2} s^{-1}); tree-covered	2.3 (1.6–5, n = 11)	11 (1.7–37, n = 10)
Red:Far red ratio; tree-covered	0.15 (0.09–0.19, n = 11)	0.19 (0.11–0.28, n = 10)
Relative air humidity (%)	80.80 ± 19.09 (n = 9)	84.01 ± 8.17 (n = 9)
Maximum temperature (°C)	24.6 ± 1.4 (n = 10)	29.2 ± 2.2 (n = 10)
Minimum temperature (°C)	9.5 ± 2.5 (n = 10)	16.7 ± 2.0 (n = 10)

bimonthly from August 2007 to May 2009. The equipment used at each site were: two max–min thermometers, a digital thermo hygrometer, a quantum sensor, LI-190SA, coupled to a Li-1000 data logger, a Li-Cor PAR sensor, and a Skye quantum sensor for R:FR ratio measurements. We recorded maximum and minimum humidity during field-work sessions. Light was measured from 1100 to 1400 hours on cloud-free days in different places of the forests with paired measures of tree-covered and open conditions. Precipitation data was obtained from two meteorological stations (INPE) near the study sites (distance: approx. 100 m from the sealevel site and approx. 10 km from the montane site; Plataforma de coleta de dados, Centro de Previsão de Tempo e Estudos Climáticos—CPTEC/INPE (2010); Projeto "Estudos da Previsibilidade de Eventos Meteorológicos Extremos na Serra do Mar").

The temperature in the montane site is lower than at sealevel and varies from 4°C in the winter to 27°C in the summer (Table 1; Fig. 1a), the annual mean precipitation is >2,000 mm, the dry season (June–August) precipitation totals 60 mm or less (Setzer 1966; Fig. 1b), and the VPD (vapour pressure deficit) of the forest is 0.37 kPa. At the sea-level site, the temperatures varies from 12°C in the winter to 32°C in the summer (Table 1; Fig. 1a). Annual mean precipitation is >2,200 mm, but is 80 mm or less in the dry season (Setzer 1966; Fig. 1b), while the forest VPD is 0.44 kPa. The relative air humidity is similar at both sites (Table 1). Finally, the understory at the montane site is more shaded than is the sealevel site, with generally less photosynthetically active radiation and a lower red:far red ratio (Table 1).

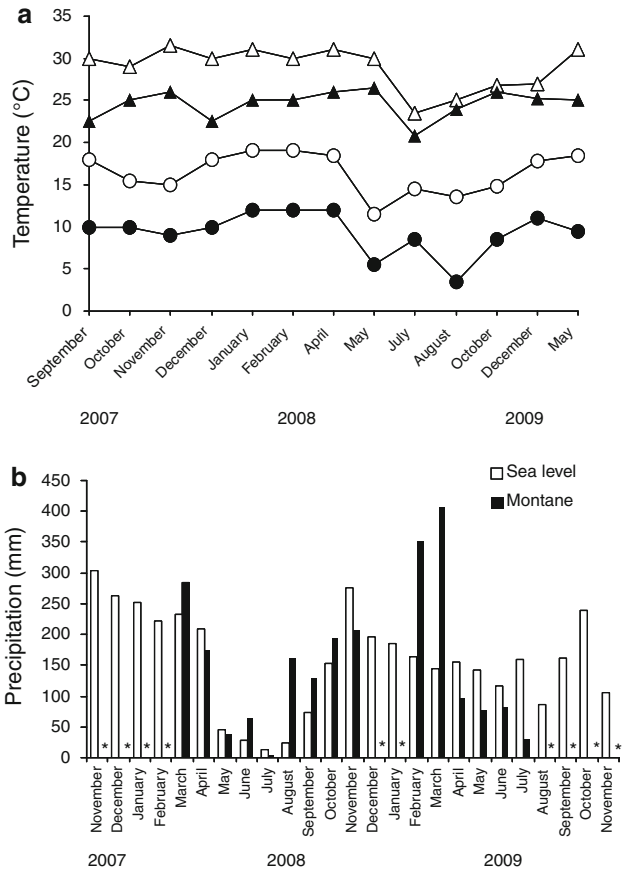

Fig. 1 **a** Maximum (*triangles*) and minimum (*circles*) temperatures (°C) from measurements in the sea level (*open symbols*) and montane sites (*filled symbols*). **b** Precipitation (mm) from meteorological stations near the sea level and montane sites; *asterisk* indicates that data were not available for all months at the montane site. (Source: "Plataforma de coleta de dados, Centro de Previsão de Tempo e Estudos Climáticos—CPTEC/INPE (2010)" for precipitation data)

Chemical characteristics of substrates

Samples of soil, decaying wood and bark from all patches where diaspore bank samples were collected were dried at 40°C for 72 h. Bark and decaying wood were ground and stored. We measured pH in all samples using 1 g suspended in 5 mL of deionised water overnight at 27°C (Farmer et al. 1990). Combined samples of each substrate type per site and season (n = 12) were chemically analyzed for available nutrients (soil) or total concentrations (bark and decaying wood) by the Laboratory of Soil Fertility (CENA-USP; Silva 1999). Both macronutrients (N, P, K, Ca, Mg and S) and micronutrients (Fe, Cu, Zn and Mn) were measured.

Diaspore bank sampling

One area (1 ha) was studied at each site per forest (sealevel and montane) and sub-divided into 100 plots of 100 m^2 each. We collected samples of soil, decaying wood and tree bark. Leaves are also important for bryophytes in tropical rain forests (Gradstein et al. 2001), but were excluded because of their short lifespan. We randomly selected 31 (montane) and 32 (sealevel) plots and collected a sample of 150 cm^2 of soil, decaying wood and bark in each plot using a knife and shovel. Given the short effective dispersal distances in bryophytes (Miles and Longton 1992; Sundberg 2005), the collecting scheme means that the samples are independent units in terms of spore input. The soil layer corresponded to the first 3 cm below the litter layer (which is usually about 5 cm thick). Bark samples were taken from the outer layer from the tree base to 150 cm in height. Decaying wood was collected from the outer 2 cm on fallen wood with stages of decay from 3 to 5 (Pyle and Brown 1999). After each sample, the shovel and knife were carefully cleaned. Samples were collected where there were no visible bryophyte plants (adults or juveniles gametophytes). Each sample was separately put in a black plastic bag and immediately brought to the laboratory. We collected in both the dry (August 2007) and rainy (January 2008) seasons.

Growth conditions

The samples were homogenized and put in 150-cm^2 containers on top of a fine vermiculite layer to keep the samples moist, and had a substrate thickness of about 1 cm. The containers were covered with transparent plastic bags and kept humid using distilled water during the experiment (Bisang 1995). Initially, we conducted experiments in growth chambers with temperatures from 20° to 25°C, a photoperiod of 12 h and a PAR of approximately 20 µmol m^{-2} s^{-1} (fluorescent lamps). These conditions were intended to simulate field conditions in the understory. After 6 months, when plants were established, we transferred the containers to a growth room with artificial and natural light, temperatures ranging from 18° to 27°C, a photoperiod of 12–14 h (fluorescent lamps were responsible for 12 h light, but in the summer natural light prolonged this to about 14 h), and PAR varying from 40 to 100 µmol m^{-2} s^{-1}. The containers were repositioned every 7th day to remove the effects of fixed spatial position in light intensity.

Species identification

We monitored shoot emergences of morphospecies from each sample monthly under a dissecting microscope. After 1 year, when many plants were sexually mature, we identified their species (in some cases genus or family). Nomenclature follows Goffinet et al. (2008) for mosses and Crandall-Stotler et al. (2008) for liverworts. The number and occurrence of species were assessed from the dry and rainy season separately, and we also counted, as far as possible, the number of shoots per species.

Bryophyte species were grouped by phylum (mosses—Bryophyta and liverworts—Marchantiophyta) and breeding system (monoicous—two sexes together in the same gametophore; dioicous—sexes in different gametophores; and polyoicous—the same species with two different breeding systems;ollowing Allen and Magill 1987). Data on breeding systems were available in Gradstein et al. (2001) and references therein. We used information from the literature (Gradstein et al. 2001 and references therein), field and laboratory observations to characterize the species in relation to their frequency of sporophytes and gemmae or gemmae-like propagules in two classes: "present to common" or "lacking to rare" following Jonsson (1993).

Occurrence in extant vegetation

We collected 244 and 167 bryophyte samples at the sealevel and montane sites, respectively, from bark and decaying wood in the same plots as used for diaspore bank sampling. These samples were preliminarily identified, but many could only be identified to family. In addition, we used information from Visnadi (2005) and preliminary data from a floristic survey (N.D. Santos, personal communication). Since no complete and quantitative bryophyte survey exists from these sites, we assigned a rough occurrence ranking of the species on a scale from 1 (least frequent) to 10 (most frequent) for a comparison of their occurrence in the diaspore bank.

Data analysis

We used generalized linear models (Glim) assuming a Poisson distribution and log-link function to test the effects of site, substrate and season on the number of species in the diaspore bank. The models were evaluated using analysis of deviance with the Wald test.

To analyze the abundance (number of shoots emerging from a sample) in the diaspore banks, we used general linear models (GLM), in which the "shoot number" variable was log $(x + 1)$-transformed prior to using analyses of variance (factorial ANOVAs).

First, we analyzed all microhabitat effects (site, substrate and season) on all species, and on each species category (monoicous mosses, monoicous liverworts, dioicous mosses and dioicous liverworts). The few polyoicous species were not included in these analyses. The "site" and "substrate" variables were treated as fixed factors, and

Table 2 Macro- and micronutrients (decaying wood and bark), available macro- and micronutrients (soil) and pH of substrates by site and season

Sample	pH Mean ± SD	N (g kg^{-1})	P (g kg^{-1})	K (g kg^{-1})	S (g kg^{-1})	Ca (g kg^{-1})	Mg (g kg^{-1})	Cu (mg kg^{-1})	Fe (mg kg^{-1})	Mn (mg kg^{-1})	Zn (mg kg^{-1})
Montane—dry											
Decaying wood	3.82 ± 0.51	9.60	0.200	0.570	1.110	3.310	0.830	5.67	433.50	193.90	17.40
Bark	4.43 ± 0.16	13.00	0.270	2.050	2.660	4.540	0.960	11.13	358.10	237.30	21.90
Soil	3.46 ± 0.17	5.65	0.040	0.012	0.023	0.004	0.004	0.56	354.68	11.98	2.92
Sea level—dry											
Decaying wood	3.98 ± 0.54	6.40	0.160	0.540	0.660	4.400	1.050	3.18	381.60	347.90	16.90
Bark	3.83 ± 0.61	10.10	0.260	0.590	1.280	2.440	0.970	8.95	300.60	57.30	11.10
Soil	3.56 ± 0.28	2.38	0.025	0.025	0.020	0.011	0.006	0.15	192.08	5.70	1.93
Montane—rainy											
Decaying wood	4.08 ± 0.59	9.90	0.200	0.570	1.050	3.360	1.050	5.32	320.70	222.60	20.10
Bark	4.61 ± 1.21	11.40	0.280	2.130	2.390	4.940	1.280	14.28	93.90	227.90	21.80
Soil	3.53 ± 0.24	6.87	0.060	0.008	0.038	0.003	0.002	0.57	319.47	19.06	3.80
Sea level—rainy											
Decaying wood	3.95 ± 0.79	7.40	0.160	0.510	0.780	4.240	1.000	3.95	249.00	204.00	16.40
Bark	3.74 ± 0.49	9.10	0.190	0.710	1.420	2.670	1.090	7.44	275.00	54.40	9.90
Soil	3.43 ± 0.18	3.35	0.025	0.020	0.019	0.011	0.006	0.14	268.55	2.92	2.23

Mean ± SD; n = 31 and 32 for montane and sea level, respectively

"species" as a random factor. Since "season" did not affect the general results, we removed it from further analyses and graphs.

To test the effect of pH, we used the same models as above but added the covariate pH. We also analyzed separately the effects of pH on the number of species and shoots using linear regressions. All analyses were conducted using Statistica version 8.0 (StatSoft) software.

Results

Chemical characteristics of substrates

In general, substrates from sea level had lower values of all nutrients than substrates from the montane site (Table 2). Bark generally contained more nutrients than decaying wood. In both seasons, large differences were observed in N, K, S, Ca, Cu and Mn values between the sea level and montane sites for bark and decaying wood. Calcium and manganese were higher in bark than in decaying wood in the montane site, but at sea level these nutrients were higher in decaying wood than in bark. We found lower potassium levels in sea level bark than in montane (Table 2).

pH values differed significantly by substrate (Wald test = 56.54; $P < 0.001$) and site (Wald test = 9.82; $P = 0.002$), and there was a significant substrate-site interaction (Wald test = 23.44; $P < 0.001$). The pH values were highest in bark, followed by decaying wood and soil (Table 2). In general, pH values for decaying wood and soil were similar at both sites, but bark pH values at sea level were low, contributing to a difference in pH between the sea level and montane sites. These pH differences were probably associated with different levels of Ca, Mn and K recorded in bark and decaying wood from both sites.

Total number of species

We found a total of 85 taxa (64 identified at species level) of bryophytes (58 montane, 53 sea level) from the three different substrates. Of these, 45 were mosses and 13 liverworts at the montane site and 31 mosses and 22 liverworts at sea level. Considerably more species were found in bark at both sites (Fig. 2a; 46 montane, 42 sea level; 68 total) and decaying wood (42 and 34; 55 total) than in soil (18 and 19; 22 total). The patterns were similar for the two seasons. Monoicous species were more numerous than dioicous (Fig. 2b). The two sites had similar numbers of monoicous (30 montane, 30 sea level), dioicous (25 and 19) and polyoicous species (3 and 4).

The most abundant species were, in decreasing order, *Isopterygium subbrevisetum*, *Syrrhopodon incompletus*, *Octoblepharum albidum*, *Trichosteleum papillosum* (mosses), *Riccardia digitiloba* and *Telaranea nematodes* (liverworts) at sea level; and *Isopterygium subbrevisetum*, *Syrrhopodon prolifer*, *Trichosteleum pusillum*, *Campylopus julicaulis*, *Syrrhopodon gaudichaudii* (mosses) and

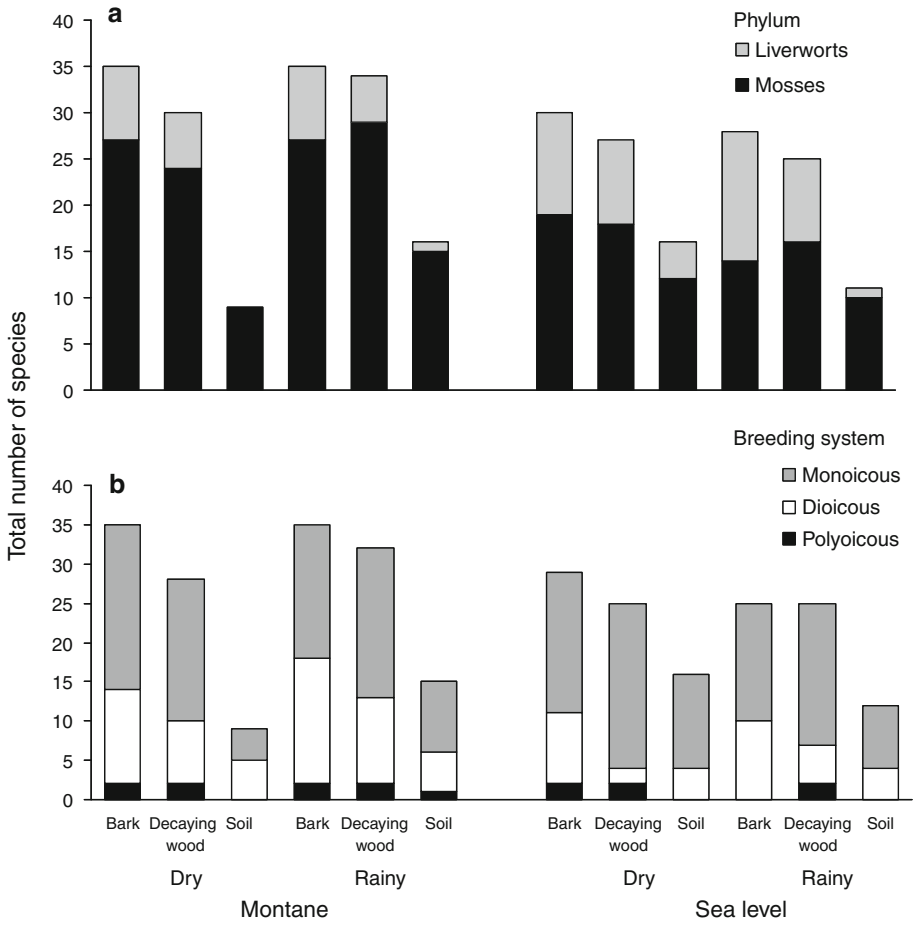

Fig. 2 Total number of moss and liverwort species (**a**), and monoicous, dioicous and polyoicous species (**b**) emerged from bark, decaying wood and soil collected in a montane and sea level site of a Brazilian Atlantic Forest, in the dry and rainy seasons

Riccardia digitiloba (liverwort) at the montane site (Table ESM1). Of these species *Syrrhopodon* spp. and *Campylopus julicaulis* are dioicous, while the others are monoicous.

Number of species per patch

The number of species per patch differed significantly among the three substrates at both sites, with a higher number generally found in decaying wood followed by bark then soil samples with lower values (Wald test = 195.176, $P < 0.001$; Fig. 3). The number of species per patch did not differ by site (Wald test = 1.306, $P = 0.253$), but the interaction between substrate and site was significant (Wald test = 9.117, $P = 0.010$), mainly because of a higher number of species in decaying wood in the montane site (Fig. 3). There was no effect by collection season on the number of species (Wald test = 2.252, $P = 0.133$).

The substrate type had significant effects on mosses and liverworts with different breeding systems (Table 3). There were more species of mosses than liverworts per patch at both sites, with the highest number in decaying wood (Fig. 4a–d). Proportionally, mosses had considerable numbers of species in the montane site (Fig. 4a, b), while

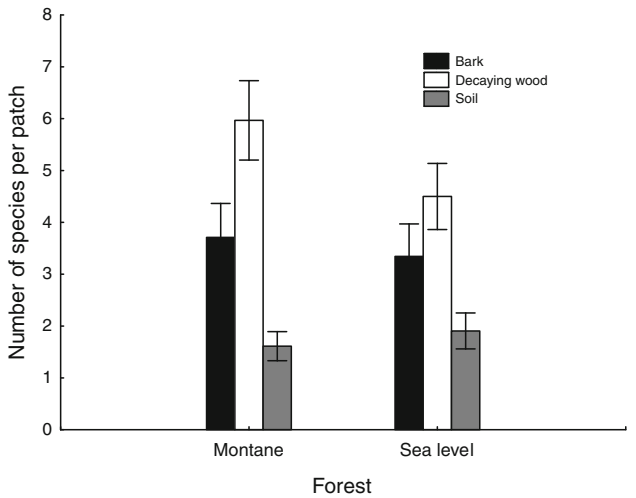

Fig. 3 Number of bryophyte species emerged per patch (150 cm^2) from bark, decaying wood and soil collected in a montane and sea level site of a Brazilian Atlantic Forest. Data are mean number of species; *error bars* ±1SE

liverworts were more noticeable at sea level (Fig. 4c, d). There were generally more monoicous than dioicous species at both sites, with a higher percentage of monoicous species among the mosses (Fig. 4a). The high number of

Table 3 GLIM analyses of the effect of site, season and substrate on the number of species per patch of mosses and liverworts with two breeding systems, using Poisson distribution with a log link function

Source	*df*	Monoicous mosses		Dioicous mosses		Monoicous liverworts		Dioicous liverworts	
		Wald test	*P*	Wald test	*P*	Wald test	*P*	Wald test	*P*
Site (S)	1	2.206	0.137	24.284	**<0.001**	0.647	0.421	0.274	0.600
Season (Seas)	1	0.054	0.816	3.785	0.051	0.016	0.898	0.401	0.526
Substrate (Sub)	2	100.51	**<0.001**	47.592	**<0.001**	30.453	**<0.001**	16.161	**<0.001**
S × Seas	1	0.785	0.375	0.064	0.801	0.019	0.888	1.495	0.221
S × Sub	2	8.711	**0.013**	14.450	**0.001**	4.157	0.125	1.046	0.592
Seas × Sub	2	1.352	0.508	3.146	0.121	0.860	0.650	1.046	0.592
S × Seas × Sub	2	0.193	0.908	2.334	0.321	0.259	0.878	3.897	0.142
Scaled deviance		378		366		378		366	
df		366		366		366		366	
Scaled deviance/*df*		1.03		1		1.03		1	

P values <0.05 are in bold. Values of scaled deviance/*df* up to 1.5 indicate a good model for the analysis

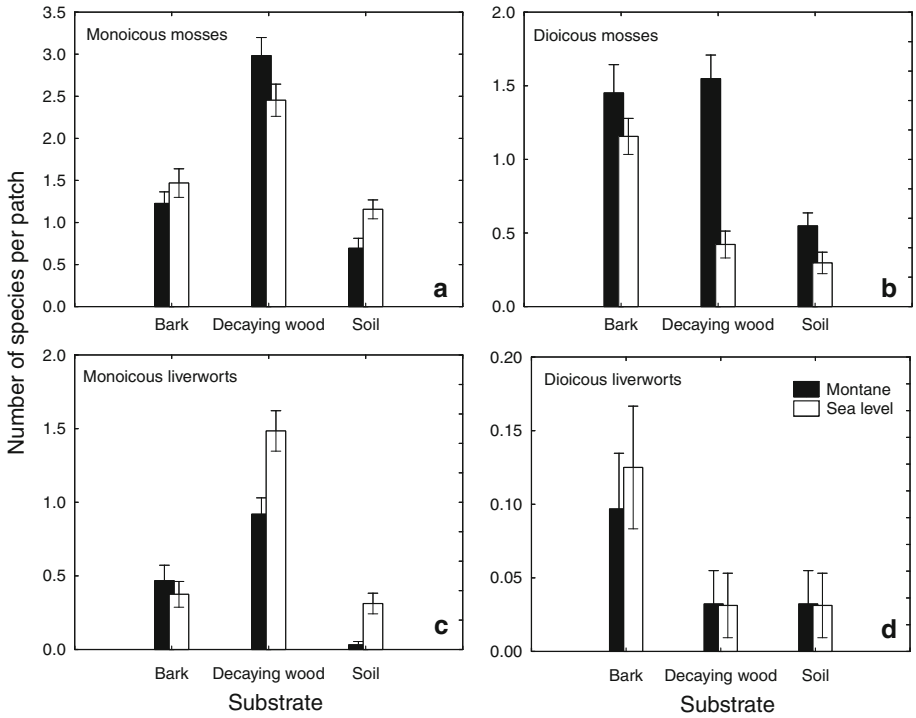

Fig. 4 Number of monoicous moss and liverwort species (**a**, **c**), and dioicous moss and liverwort species (**b**, **d**) emerged per patch (150 cm^2) from bark, decaying wood and soil collected in a montane and sea level site of a Brazilian Atlantic Forest. Data are mean number of species; *error bars* ±1SE; note different scales of *y*-axes

monoicous and dioicous mosses in decaying wood in the montane site contributed to the significant site–subtrate interactions (Fig. 4a, b; Table 3). The site had a significant effect only on dioicous mosses (Table 3).

Number of shoots

The number of shoots increased slowly during the first 5 months of incubation, and final data were collected after 7 months (Fig. 5a–d). During the first 5 months of incubation, shoot numbers varied around 10 and 50 per patch at the montane and sea-level sites, respectively. After 7 months, these numbers increased to around 150 shoots per patch at both sites, possibly because of the change in light conditions (see "Growth conditions" below). It was not possible to count shoots after 7 months due to shoot and species intermixing. At the sea-level site, species with the highest number of shoots were the mosses *Isopterygium* spp., *Pterogonidium pulchellum*, *Octoblepharum albidum*, *Syrrhopodon* spp., *Trichosteleum papillosum*, Pilotrichaceae spp. (mainly *Callicostella pallida/rufescens*), and the liverworts Lejeuneaceae spp. (mainly *Cheilolejeunea* spp. and *Ceratolejeunea* spp.), *Riccardia digitiloba*, *Telaranea nematodes and Arachniopsis monodactyla*. Abundant at the

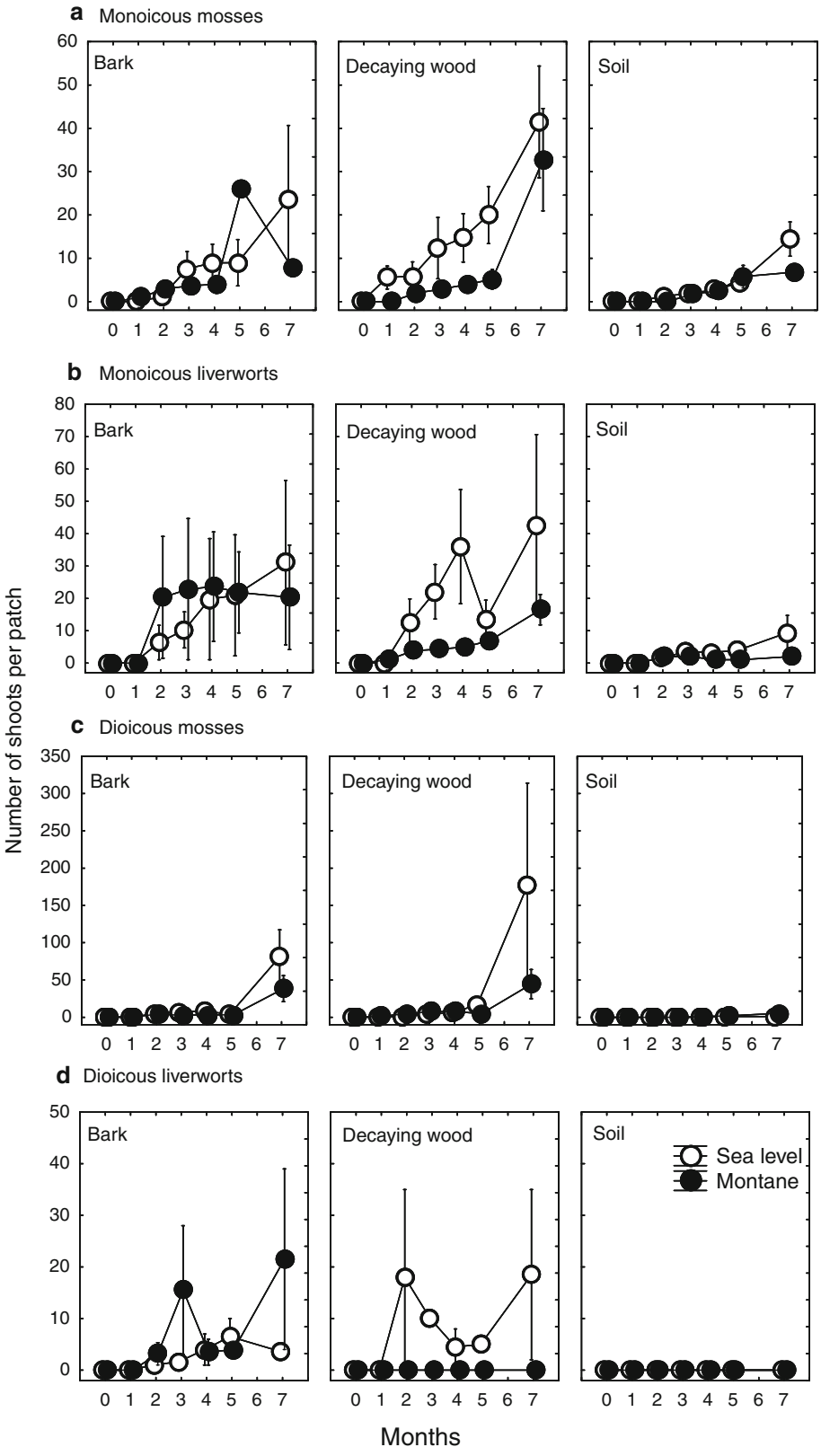

Fig. 5 Number of shoots of liverwort and moss with different breeding systems (**a**, **b** monoicous; **c**, **d** dioicous) emerged per patch (150 cm^2) from bark, decaying wood and soil collected in a montane and sea level site of a Brazilian Atlantic Forest. Data are mean number of shoots in each species per sample; *error bars* ±1SE; note different scales of *y*-axes

montane site were the mosses *Isopterygium* spp., *Syrrhopodon* spp., *Trichosteleum pusillum*, Pilotrichaceae spp. (mainly *Thamniopsis incurva*), *Pyrrhobryum spiniforme*, and the liverworts *Riccardia digitiloba*, Lejeuneaceae spp. (mainly *Metalejeunea cuculata*), *Telaranea nematodes* and *Lophocolea* spp. All these species are monoicous, with the

Table 4 Number and proportion of sporophytes or gemmae-producing species, monoicous and dioicous mosses and liverworts from diaspore banks and vegetation at a montane and sea-level site of a Brazilian Atlantic Forest

	Montane		Sea level	
	Vegetation	Diaspore bank	Vegetation	Diaspore bank
Monoicous mosses				
Number of species	17	22	15	19
Sporophyte-producing (%)	100	100	100	100
Gemma-producing (%)	7	5	13	11
Dioicous mosses				
Number of species	14	21	12	12
Sporophyte-producing (%)	21	35	25	27
Gemma-producing (%)	64	60	66	73
Monoicous liverworts				
Number of species	5	9	8	11
Sporophyte-producing (%)	50	71	87	55
Gemma-producing (%)	50	71	37	50
Dioicous liverworts				
Number of species	4	3	5	7
Sporophyte-producing (%)	50	33	20	0
Gemma-producing (%)	25	33	20	33

exception of *Syrrhopodon* spp. (dioicous) and *Ceratolejeunea* spp. (polyoicous).

The number of shoots of each species per patch resembled the pattern recorded for the number of species per patch, i.e., decaying wood had highest values, followed by bark then soil (Fig. 5a–d; Wald test = 8.53, $P = 0.001$). The substrate had a significant effect only on monoicous mosses (Wald test = 5.12, $P = 0.017$), but no effect was recorded for dioicous mosses and liverworts. There were more moss shoots than liverwort when recording ended (after 7 months), with a strong contribution from dioicous mosses at sea level (Fig. 5c). No significant effect of site or site-interactions were observed on moss or liverwort shoots. Monoicous species were generally more abundant, followed by dioicous then polyoicous ones (data not shown).

Effect of substrate pH

Main significant effects of pH were detected on species number for monoicous mosses (Wald test = 4.55, $P = 0.030$), dioicous mosses (Wald test = 7.18, $P = 0.007$), monoicous liverworts (Wald test = 24.87, $P \leq 0.001$) and dioicous liverworts (Wald test = 5.50, $P = 0.019$). However, the explanatory power of pH was low. For instance, we only detected significant, but weak, negative effects of pH on the number of monoicous liverwort species in decaying wood from the sea-level and montane sites ($y = 3.48 - 0.48x$, $R^2 = 0.09$ and $y = 2.81 - 0.47x$, $R^2 = 0.09$, respectively), and a weak positive effect on the number of monoicous mosses in decaying wood from the montane site ($y = -0.44 + 0.90x$, $R^2 = 0.10$). The analyses of shoot numbers indicated no pH effect, neither directly nor from interactions.

Relationship between diaspore bank and vegetation

In both the vegetation and in the diaspore bank, moss species were more numerous than liverworts, and monoicous species were more numerous than dioicous species (Table 4; χ^2 tests showed no differences in these relationships between vegetation and diaspore bank). Monoicous species with sporophytes, as well as dioicous species with gemmae, were well represented at the two sites, both in the diaspore bank and the vegetation (Table 4). Among gemmae-producing liverworts, monoicous species were more numerous than dioicous ones, both in the diaspore bank and in the vegetation. Both liverworts and mosses dioicous species with gemmae were more abundant in the diaspore bank than in the vegetation, in contrast to gemmae-producing monoicous species.

In general, many species that were well represented in the diaspore bank were also found in the vegetation (Table ESM1). A few species were well represented in the vegetation but not in the diaspore bank, and these were mainly dioicous species, including both mosses (*Meteoridium remotifolium* at both sites) and liverworts (*Ceratolejeunea cornuta*, *Plagiochila disticha*, *Bazzania phyllobola* at sea level). The monoicous liverwort *Riccardia digitiloba*, which is commonly found with gemmae and sporophytes, was abundant in the diaspore bank, but not in the vegetation. *Sphagnum* cf. *recurvum*, from the montane site, was the only species in the diaspore bank that was not observed in the vegetation.

Discussion

We have described diaspore banks that represent the extant vegetation rather well, somewhat contrasting with diaspore banks in temperate regions, which have a low proportion of species commonly found in the vegetation. Diaspores found mostly at bark and decaying wood are probably short-lived, in contrast to the very long-lived diaspores found in the soil samples in temperate regions (During et al. 1987; Bisang 1995; Ross-Davis and Frego 2004).

We corroborated our hypotheses at least partially: mosses were more numerous than liverworts, and monoicous species were more numerous than dioicous ones. Dioicous species were proportionally more common at the montane site, and liverworts at sea level. The substrates bark and decaying wood supported the highest numbers of species. However, the effects of substrate pH were very weak for the different groups, and seasonal differences were not important.

Effects of habitat and season

The distribution of the diaspore bank among different substrates corresponds with surveys of bryophytes in tropical rain forests, with high richness of epiphytic, saxicolous, epixylic, epiphyllous but few terricolous species (Visnadi 2005; Santos and Costa 2008). The scarcity of bryophytes on the forest floor is due to a thick layer of leaf litter covering the soil (Frahm and Gradstein 1991). This is different from bryophytes in boreal forests, which abundantly cover soils and have a rich diaspore bank (Jonsson 1993). Our results also contrast with findings from fire-prone savanna plots of Zimbabwe (During 2007) and forests in Spain (During et al. 1987), where the bryophyte vegetation was sparse, but the diaspore bank remarkably rich and partly consisting of species with very long-lived diaspores.

There were only small differences between the montane and sea-level diaspore banks, such as a higher number of species in decaying wood at the montane site. Since bryophyte species richness generally increases from lowland to montane tropical rain forests (Frahm and Gradstein 1991), and more species are present in bark and decaying wood in these forests, a site–substrate interaction effect was expected. It was further expected given the higher values of nutrients from bark and decaying wood in the montane compared to the sea-level site. We did find such an interaction for the mosses, but it appears that the microclimatic differences between the sites do not have a very strong effect on the diaspore bank. Although there is no marked dry season, there is a peak in spore dispersal mainly from April to October (Maciel-Silva, unpublished data), but this did not cause a seasonal pattern in the diaspore bank.

The role of breeding system and phylum, and the relationship to extant vegetation

Breeding system is important to determine the diaspore bank composition, with a high contribution of monoicous species. These findings differ from the dominance of dioicous species in the vegetation from bryophyte surveys in the same forest (Visnadi 2005). The vegetation data reveal approximately 64 and 36% of dioicous and monoicous species, respectively (from 353 species; Visnadi 2005) in the vegetation against 45 and 55%, respectively, in the diaspore bank (present study). The vegetation contains a number of rare dioicous species that can be found in an intensive vegetation survey, but may easily be missed in diaspore bank sampling.

Monoicous species seem to be favored by their frequent sporophyte production (Longton 1992). In addition, their capsules contain a high number of spores (thousands to millions, depending on species; Frahm 2008). Although the relationship between frequent sporulation and monoicism in mosses was recently questioned in an analysis accounting for phylogeny (Crawford et al. 2009), the correlations remained significant when the species were analyzed as independent data points. Interestingly, we recorded a higher species number of monoicous liverworts with gemmae, compared to dioicous species with gemmae, in the diaspore bank. It is surprising that in our systems many monoicous liverworts invest largely in asexual reproduction even when they are able to produce many sporophytes and spores. This may be a strategy to compensate for the observations that spores of liverworts are more sensitive to high and low pH than spores and gemmae of mosses (Löbel and Rydin 2010). Moreover, the higher contribution in the bank than in the vegetation of dioicous species with gemmae suggests an important role of asexual diaspores in these tropical forest diaspore banks.

The frequency of both monoicous and dioicous mosses commonly producing sporophytes and gemmae was high in the diaspore bank. That is, mosses with success in the diaspore banks seem to invest strongly in spores or specialized asexual structures. In addition, differences such as high germination and protonemal growth rate, as well as tolerance to desiccation in mosses, and fast transition from protonema to shoot stage in liverworts (Maciel da Silva et al. 2006; Löbel and Rydin 2010), may explain the dominance of mosses over liverworts. Beyond this, many shoots can develop clonally from the large filamentous protonema of mosses, while the globose protonema of liverworts develops into a single shoot (Nehira 1983).

Weak influence of pH

pH values recorded for the main substrates are related to degree of decay and acidic organic matter present, decreas-

ing from bark to decaying wood and soil. The low pH values recorded in the sea-level site (pH 3.7–3.8) are exceptional for pH of bark in tropical rain forests (pH 4–5; ter Steege and Cornelissen 1989) and are linked to the low amounts of calcium. However, despite the marked differences of pH between bark from the sea-level and montane sites, neither the number of species nor shoot production was strongly affected by pH. Only two weak effects were noted: monoicous liverworts and mosses responded negatively and positively, respectively, to increased pH. The high humidity in tropical rain forests possibly counteracts the negative effect of low pH (cf. Löbel and Rydin 2010).

The dynamics of the bryophyte diaspore banks in tropical rain forests

Based on our results, we propose a conceptual model for the discussion of the dynamics of the bryophyte diaspore banks in tropical rain forests (Fig. ESM1): spores and asexual diaspores reach the substrates after short- or long-range dispersal by wind, rain or animals (Frahm 2008; Rudolphi 2009). Microscopic forms (post-germination stages such as protonema and gametophytic buds or small shoots) may develop and remain inactive due to lack of suitable conditions (see references in Schofield 1981; Thomas et al. 1994; Proctor et al. 2007). The contribution to the diaspore bank is in decreasing order: (1) spores and (2) asexual diaspores from near sources, (3) distant spores and (4) distant asexual diaspores (Miles and Longton 1990; Pohjamo et al. 2006). In the case of long-range dispersal of asexual diaspores, animal vectors can be important (Parsons et al. 2007; Rudolphi 2009). In our system, mosses and liverworts distinctly contribute to the banks, with more monoicous mosses and fewer dioicous liverworts. Decaying wood and bark contain many species and high numbers of diaspores, while soil supports few diaspores that are also rapidly buried under a thick leaf litter.

Diaspores can be activated under suitable conditions, with a higher contribution of mosses than liverworts, since many shoots can develop from each moss protonema and because of the clonal growth of mosses during the protonemal phase. Losses are caused by decay, predation, parasitism and burial. In the latter case, persistent diaspores can emerge after soil disturbance (e.g., treefall).

We do not know the true longevity of the diaspores present in this bank, but morphological traits such as green color of spores (high metabolism associated with low longevity; Lloyd and Klekowski 1970) in many species from tropical forests, and low survival of fragments over a long time (due to chlorosis), suggest that these diaspore banks are transient rather than persistent. Assays in the laboratory suggest a few months of longevity under dry conditions. The viability of small spores and asexual, specialized diaspores decreases from around 80–100% to lower than 30 and 70%, respectively, after 50 days (Löbel and Rydin 2010). Spores of epiphytic and epixylic species have their viability reduced from around 90% to near zero after 48–240 days and 25–30 days, respectively (Egunyomi 1978; Wiklund and Rydin 2004; Maciel da Silva et al. 2009). Apical gametophyte fragments maintain 80% or higher viability after 120 days in the field under dry storage (Cleavitt 2002, 2005). In contrast, spores of *Sphagnum* could retain high viability (around 70%) after 3 years of burial in peat (Sundberg and Rydin 2000), and desiccated moss tubers can germinate after more than a century (H. During, personal communication).

We propose that short-term diaspore banks of bryophytes in tropical rain forests can contribute to fast (re)establishment of many species after disturbance and during succession. Pioneer species investing highly in asexual reproduction (e.g., dioicous mosses) during the first months, or sexual reproduction (e.g., monoicous mosses) in the first year after establishment, are especially important. These surface banks should have an important role after small-scale disturbances (e.g., animal activities, treefall gaps), but since they are probably transient rather than persistent, they can be strongly affected by environmental changes such as desiccation and high irradiance.

Acknowledgments This research was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes), the Conselho Nacional de Pesquisa e Tecnologia (CNPq), and the State of São Paulo Research Foundation (FAPESP) as part of the Thematic Project Functional Gradient (Process Number 03/1259507), within the BIOTA/FAPESP Program—The Biodiversity Virtual Institute (http://www.biota.org.br). COTEC/IF 41.065/2005 and IBAMA/CGEN 093/2005 permits collect. We are grateful to Jan-Peter Frahm, William Buck, Thais F. Vaz-Imbassahy and Nivea D. Santos for help with identification, verification and information about species, and to Adalberto J. Santos and Luciano Pereira for help in the field and laboratory. Sincere thanks to Takashi Muraoka (Laboratório de Fertilidade do Solo, CENA-USP) for nutrient analyses. We thank Heinjo During and Sebastian Sundberg for helpful comments on the manuscript, and Scott Spellerberg for revising the English.

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Table ESM1. Occurrence rank of bryophyte taxa from the diaspore banks (in bark, decaying wood and soil) and vegetation (V; rank from 1 to 10, where 1 means least frequent species) in two sites of a Brazilian Atlantic Forest. Data from both seasons are combined. Species are classified according to phylum (Ph; M = mosses, L = liverworts) and Breeding system (BS; M = monoicous species, D = dioicous species, P = polyoicous, and M/D = both monoicous and dioicous species present).

	Montane								Sea level						
Species	**BS**	**Ph**	Bark	DW	Soil	**Total**	**V***	**Species**	**BS**	**Ph**	Bark	DW	Soil	**Total**	**V***
Number of patches	-	-	62	62	62	**186**	-	Number of patches	-	-	64	64	64	**192**	-
Acroporium exiguum	M	M	1	1	0	**2**	-	*Acroporium exiguum*	M	M	2	1	0	**3**	3
Actinodontium spruce	D	M	17	10	1	**28**	-	*Actinodontium sprucei*	D	M	1	1	0	**2**	-
Aerobryopsis cf. *capensis*	D	M	3	0	0	**3**	-	*Arachniopsis monodactyla*	M	L	1	8	0	**9**	3
Bazzania heterostipa	D	L	4	0	0	**4**	3	*Bazzania heterostipa*	D	L	2	0	0	**2**	5
Bryopteris fillicina	P	L	0	0	0	**0**	4	*Bazzania phyllobola*	D	L	1	0	0	**1**	9
Bryum cf. *limbatum*	D	M	3	1	2	**6**	2	*Bryopteris diffusa*	P	L	0	0	0	**0**	5
Callicostella depressa	M	M	6	16	0	**22**	3	*Callicostella depressa*	M	M	0	3	1	**4**	-
Callicostella pallida	M	M	1	3	0	**4**	-	*Callicostella pallida*	M	M	4	4	3	**11**	-
Callicostella rufescens	M	M	0	1	0	**1**	-	*Callicostella rufescens*	M	M	2	14	1	**17**	3
Calypogeia peruviana	M	L	0	1	0	**1**	3	Calymperaceae sp.1	D	M	1	0	0	**1**	-
Campylopus dichrostis	D	M	5	5	0	**10**	3	*Calypogeia peruviana*	M	L	1	4	1	**6**	-
Campylopus filifolius	D	M	6	11	0	**17**	3	*Campylopus julicaulis*	D	M	0	0	1	**1**	3
Campylopus julicaulis	D	M	4	20	24	**48**	5	*Ceratolejeunea cornuta*	P	L	1	2	0	**3**	10
Cyclodictyon varians	M	M	2	3	0	**5**	3	*Ceratolejeunea cubensis*	P	L	6	2	0	**8**	4
Fissidens angustifolius	M	M	3	3	4	**10**	2	*Cheilolejeunea adnata*	M	L	2	0	0	**2**	-
Fissidens cf. submarginatum	M	M	0	0	1	**1**	-	*Cheilolejeunea* cf. *acutangula*	M	L	1	0	0	**1**	2
Haplolejeunea cucullata	M	L	2	0	0	**2**	-	*Cheilolejeunea discoidea*	M	L	4	9	0	**13**	-
Hymenodon aeruginosus	D	M	1	0	2	**3**	-	*Cheilolejeunea* sp.1	M	L	1	0	0	**1**	-
Hypopterygium tamarisci	M	M	4	1	0	**5**	3	*Fissidens angustifolius*	M	M	0	0	2	**2**	-
Isopterygium subbrevisetum	M	M	28	50	19	**97**	5	*Groutiella* sp.1	D	M	0	1	0	**1**	-
Isopterygium tenerum	M	M	1	6	11	**18**	5	*Haplolejeunea cucullata*	M	L	0	1	0	**1**	-

Table ESM1. Continued.

Kurzia capillaries	D	L	1	0	0	**1**	-	*Helicodontium capillare*	M	M	1	0	0	**1**	-
Lejeuneaceae sp.1	M/D	L	1	1	0	**2**	-	*Isopterygium subbrevisetum*	M	M	34	49	39	**122**	5
Lepidopilum cf. *scabrisetum*	P	M	4	1	0	**5**	-	*Isopterygium tenerum*	M	M	2	3	6	**11**	5
Lepidopilum ovalifolium	D	M	6	3	0	**9**	-	*Lejeunea flava*	M	L	0	0	0	**0**	5
Lepidopilum sp.1	M/D	M	0	0	1	**1**	-	*Lejeunea laetevirens*	M	L	0	0	0	**0**	3
Leucobryum cf. *martianum*	D	M	0	1	0	**1**	-	*Lejeunea* sp.1	M/D	L	2	1	0	**3**	-
Leucobryum crispum	D	M	3	1	1	**5**	3	Lejeuneaceae sp.2	M/D	L	1	0	0	**1**	-
Leucobryum sp.1	D	M	2	1	0	**3**	-	*Leucobryum clavatum*	D	M	0	0	0	**0**	4
Leucoloma serrulatum	D	M	2	3	0	**5**	3	*Leucobryum crispum*	D	M	0	1	0	**1**	1
Leucomium strumosum	M	M	0	2	0	**2**	-	*Leucoloma serrulatum*	D	M	1	0	0	**1**	3
Lophocolea martiana	M	L	1	7	0	**8**	10	*Leucophanes molleri*	D	M	2	0	1	**3**	5
Lophocolea perissodonta	M	L	1	13	1	**15**	2	*Lophocolea martiana*	M	L	1	3	2	**6**	5
Lophocolea sp.1	M	L	0	2	0	**2**	-	*Metalejeunea cucullata*	M	L	3	3	0	**6**	-
Lopidium concinnum	P	M	0	0	0	**0**	4	*Meteoridium remotifolium*	D	M	0	0	0	**0**	8
Macrodictyum proliferum	D	M	1	0	0	**1**	-	*Mnioloma* cf. *parallelogramma*	D	L	1	0	0	**1**	-
Metalejeunea cucullata	M	L	10	0	0	**10**	-	*Neckeropsis* spp.	M	M	1	0	0	**1**	4
Meteoridium remotifolium	D	M	1	1	0	**2**	10	*Neurolejeunea breutelii*	D	L	0	1	0	**1**	-
Meteorium cf. nigrescens	D	M	0	1	0	**1**	5	*Octoblepharum albidum*	M	M	29	16	12	**57**	6
Metzgeria spp.	M/D	L	0	0	0	**0**	4	*Odontoschisma falcifolium*	D	L	2	0	0	**2**	-
Neckeropsis spp.	M	M	0	0	0	**0**	4	*Phylogonium viride*	D	M	0	0	0	**0**	3
Pallaviciniaceae spp.	D	L	0	0	0	**0**	1	*Plagiochila disticha*	D	L	2	0	0	**2**	7
Phyllogonium viride	D	M	5	0	0	**5**	3	*Plagiochila* sp.1	D	L	1	0	0	**1**	-
Plagiochila gymnocalycina	D	L	1	0	0	**1**	5	*Pterogonidium pulchellum*	M	M	4	7	5	**16**	4
Porella spp.	D	L	0	0	0	**0**	3	*Pyrrhobryum spiniforme*	M	M	0	0	0	**0**	6
Porotrichum spp.	D	M	0	0	0	**0**	3	*Radula* spp.	D	L	0	0	0	**0**	1
Pyrrhobryum spiniforme	M	M	4	18	1	**23**	10	*Riccardia digitiloba*	M	L	2	45	2	**49**	1
Radula cf. elliotii	D	L	1	0	0	**1**	-	*Schlotheimia* cf. *jamesonii*	D	M	1	0	0	**1**	-
Riccardia digitiloba	M	L	9	33	0	**42**	3	Sematophyllaceae sp.1	M	M	0	1	0	**1**	-

Table ESM1. Continued.

Sematophyllaceae sp.1	M	M	0	2	0	**2**	-	*Sematophyllum adnatum*	M	M	0	1	0	**1**	1
Sematophyllum galipense	M	M	2	0	0	**2**	4	*Sematophyllum galipense*	M	M	2	4	2	**8**	3
Sematophyllum sp.1	M	M	0	1	0	**1**	-	*Sematophyllum subpinnatum*	M	M	6	5	0	**11**	5
Sematophyllum sp.2	M	M	1	0	0	**1**	-	*Sematophyllum subsimplex*	M	M	0	12	0	**12**	5
Sematophyllum subpinnatum	M	M	2	2	0	**4**	5	*Syrrhopodon gaudichaudii*	D	M	17	3	2	**22**	4
Sematophyllum subsimplex	M	M	1	1	1	**3**	5	*Syrrhopodon incompletus*	D	M	38	16	11	**65**	5
Sphagnum cf. *recurvum*	D	M	0	0	1	**1**	-	*Syrrhopodon ligulatus*	D	M	1	1	0	**2**	1
Syrrhopodon gaudichaudii	D	M	22	18	2	**42**	8	*Syrrhopodon prolifer*	D	M	13	6	3	**22**	5
Syrrhopodon incompletus	D	M	1	0	0	**1**	2	*Telaranea diacantha*	M	L	0	0	0	**0**	5
Syrrhopodon prolifer	D	M	25	29	2	**56**	9	*Telaranea nematodes*	M	L	9	22	15	**46**	3
Telaranea nematodes	M	L	5	3	0	**8**	4	*Thamniopsis incurva*	M	M	1	0	0	**1**	4
Thamniopsis incurva	M	M	6	25	3	**34**	4	*Trichosteleum papillosum*	M	M	6	35	4	**45**	3
Thamniopsis langsdorffii	M	M	3	11	0	**14**	3	*Vesicularia vesicularis*	M	M	0	2	0	**2**	5
Thuidium tamariscinum	D	M	0	1	0	**1**	3	*Zelometeorium patulum*	D	M	0	0	0	**0**	5
Trachyxiphium guadalupense	M	M	6	16	0	**22**	2								
Trichosteleum pusillum	M	M	11	41	3	**55**	3								

** - indicates insufficient information to rank the species.*

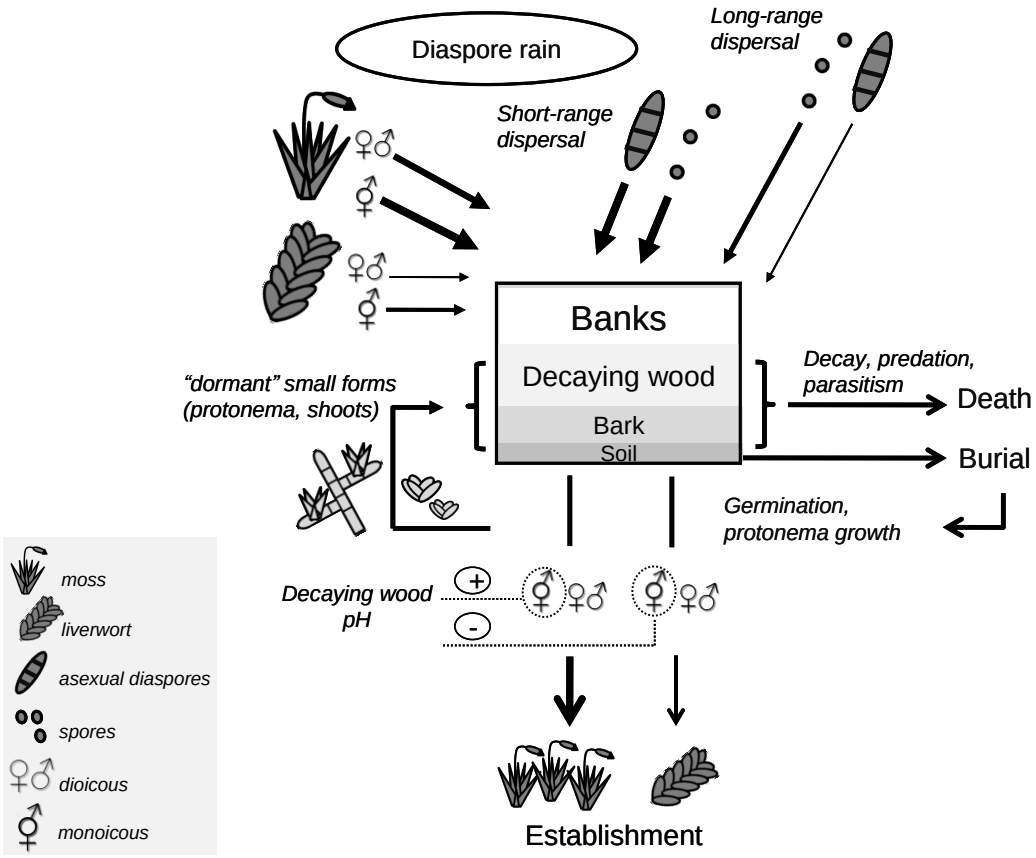

Fig. ESM1. Conceptual model of the dynamics of bryophyte diaspore banks in tropical rain forests. Arrow thickness indicates diaspore number in the diaspore rain, and number of established shoots in mosses and liverworts. Dashed lines denote weak pH effects on the monoicous species (encircled)