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Community dynamics in a species-rich patch of old-growth forest in a global changing scenario

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ABSTRACT

Ecological theory predicts that, in mature ecosystems, species richness, the number of individuals and the biomass of individuals will remain in a relatively stable state of equilibrium. The aim of this study was to test that theory. In 2001 and 2010, we conducted censuses of all trees with a circumference at breast height ≥ 10 cm in a one-hectare plot in a seasonal semideciduous old-growth forest in southeastern Brazil. We compared the two censuses in terms of species richness and diversity, computing growth, recruitment and mortality rates, as well as gains and losses of basal area. Between 2001 and 2010, species richness declined from 224 to 218 species and the basal area increased from 37.86 to 40.16 m^2 ha^{-1}. Overall turnover (the mean difference between mortality and recruitment) was lower than would be expected for a seasonal semideciduous forest, indicating stability and slight successional advance. This interpretation is supported by the observation that pioneer species and canopy species both showed higher mortality than recruitment. However, uncommon species (< 10 individuals in the 2001 census) showed higher mortality than recruitment and became rarer, whereas most species that were abundant in 2001 became more abundant by 2010. These observations, as well as the decline in species richness, although statistically not significant, match the predictions of ecological theory for scenarios in which formerly contiguous ecosystems become fragmented and the remnants become isolated within the landscape. Nevertheless, further censuses are needed in order to test the idea that the observed patterns are not explained by natural oscillations but are consequences of environmental changes related to human activity.

Key words: Community dynamics, habitat loss, immigration rate, landscape fragmentation, species richness.

Introduction

Climate change (IPCC 2007; Matesanz *et al.* 2010), habitat destruction and fragmentation (Wright 2010) threaten species richness and diversity worldwide. Because tropical forests account for the major part of terrestrial biodiversity (Millennium Ecosystem Assessment 2005), climate change is expected to have severe effects on such forests. To outline and understand the influences of global changes on forest communities, their species richness and diversity, it is necessary to conduct long term monitoring studies known as community dynamics studies (Losos & Leigh Jr. 2004).

Species composition within a given community undoubtedly varies over time (Rosenzweig 1995; Hubbell 2001; Magurran 2011). These variations depend on the disturbance regime (Connell 1978; Molino & Sabatier 2001; Machado & Oliveira-Filho 2010), ecological drift and stochasticity (Hubbell 2001).

The division of formerly contiguous forests into fragments of variable size and shape also alters the ecological processes of the natural dynamics of the forest (Tabarelli *et al.* 2004). In addition, changes in resource availability influence growth, mortality and recruitment of trees within forest communities (Ernest *et al.* 2009).

Among tropical forests, the Atlantic Forest of Brazil is one of the most diverse ecosystems (Stehmann *et al.* 2009). Due to its high degree of endemism and endangered status, it is considered a biodiversity hotspot (Myers *et al.* 2000). Once covering up to 1,500,000 km^2 (Câmara 2005), only 11% of the original Atlantic Forest remains, most of it as small secondary forest patches (Ribeiro *et al.* 2009). Species-rich old-growth forests are extremely rare.

The aim of this study is to test whether the mature tree community of the Seu Nico Forest (SNF) shows stability in the form of dynamic equilibrium over time, in terms of community dynamics, such as mortality and recruitment rates (Oliveira-Filho *et al.* 2007); species richness (MacArthur & Wilson 1967); the number of individuals or zero-sum dynamics (Hubbell 2001); and basal area per individual (Ernest *et al.* 2009).

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Methods

Study site

The SNF is a 35 ha patch of species-rich old-growth forest (20°47'44"S; 42°50'50"W) on the Bom Sucesso Farm, in the town of Viçosa, which is in the state of Minas Gerais, Brazil. The owners of the SNF state that it has never been logged (Campos *et al.* 2006). According to the Köppen climate classification system (Köppen 1948), the climate of the region is type Cwb (Peel *et al.* 2007), a humid mesothermal climate with mild, rainy summers and dry winters. The predominant soils are deeply weathered oxisols, which are found within a small-scale mosaic of inceptisols on slopes and neosols in sedimentation areas of valley bottoms. The predominant vegetation is characterized as submontane seasonal semideciduous forest (Veloso *et al.* 1991).

Data collection

Within the SNF, a 100 × 100 m (1-ha) area was marked off and divided into 100 plots of 10 × 10 m. In an initial census, conducted for all of the plots between October 2000 and March 2001 (Irsigler 2001), all trees with a circumference at breast height ≥ 10 cm—corresponding to a diameter (DBH) ≥ 3.2 cm—were tagged and identified. Because it is conventional to use diameter rather than circumference in the international literature, we will hereafter refer to the DBH. During a second census, carried out between December 2009 and February 2010, we measured the circumference of all surviving individuals within the 100 plots. Recruits (individuals that had not been tagged but met the inclusion criteria) were also tagged and identified. Specimens were collected, identified and deposited in the Herbarium of the Federal University of Viçosa (code, VIC). Species nomenclature follows the database compiled by Forzza *et al.* (2012). Species classification follows the Angiosperm Phylogeny Group III guidelines (APG III 2009).

Data analysis

To compare species richness between the two censuses, we calculated the species-area relationship using the power model proposed by Arrhenius (1921) to fit the species--accumulation curve:

$$S = cA^z \quad (1)$$

where *S* is the number of species; *A* is the area; and *c* and *z* are constants corresponding to the intercept with the y-axis (*c*) and the slope (*z*) of the linearized species-area relationship after log transformation of *S* and *A*. For the fitting, we assessed the average number of species within groups of 2, 5, 10, 25 and 50 plots, as well as within the study site as a whole (all 100 plots). Only neighboring plots were grouped.

Linearized in logarithmic space, the slope of the species--area relationship describes the difference between plots and is therefore interpreted as spatial turnover, or beta diversity (Condit *et al.* 1996). For statistical comparison of the values, we used Microsoft Excel™ to perform linear least squares regression.

For both censuses, the biodiversity indices of Simpson and Shannon-Wiener, as well as Fisher's alpha, were computed with the software EstimateS (Colwell & Coddington 1994; Colwell 2005). Statistical differences in diversity as well as in species richness, basal area and number of individuals were checked for significance by a two-sample t-test after testing for normal distribution by a Shapiro-Wilk test with STATISTCA software, version 7.0 (StatSoft Inc., Tulsa, OK, USA). Parameters were calculated for each plot.

The community dynamics were calculated as proposed by Losos & Lao (2004). To calculate the average growth rate between censuses, the increase in diameter for each tree was divided by the interval (in years) between the two censuses. The average growth rate is the average of the growth rates of all trees meeting the inclusion criteria.

The difference in the mortality rate of trees between the censuses is the natural logarithm of the proportional relationship between the number of trees tagged in the first census and that of those surviving to the second census, divided by the time between the two:

$$MR = \frac{In(\frac{N_I}{N_S})}{T} \quad (2)$$

where *MR* is the mortality rate, N_S is the number of survivors (trees that were alive in both censuses), N_I is the N_S minus the number of undetected individuals or individuals that died between the two censuses, and *T* is the average interval between censuses (in years). The rate of tree recruitment was calculated as follows:

$$RR = \frac{In(\frac{N_S + N_R}{N_S})}{T} \quad (3)$$

where *RR* is the recruitment rate, and N_R is the number of new trees appearing between censuses (i.e., recruits).

For any given plot, a loss in basal area (defined as the area below the 3.2 cm DBH level) resulted from mortality and from stem breakages. To calculate the loss in basal area between the two censuses (the total basal area of trees tagged in the first census that had died or whose basal area had otherwise been lost by the time of the second census), we employed the following equation:

$$BA_{loss} = \frac{AB_M}{T} \quad (4)$$

where BA_{loss} is the total basal area lost, and AB_M is the difference in basal area between the two censuses. Similarly, a gain in basal area was calculated as follows:

$$BA_{gain} = \frac{BA_{S2} - BA_{S1}}{T} \quad (5)$$

where BA_{gain} is the total basal area gained, BA_{S2} is the total basal area of the trees surviving from the first to the second census, and BA_{S1} is the total basal area of those same individuals in the first census. For the calculation of demographic dynamics, all stems of multi-stemmed individuals were included.

We calculated demographic dynamics not only for the community as a whole but also for different size classes, as proposed by Losos & Lao (2004): class I (DBH = 3.2-9.9 cm); class II (DBH = 10-29.9 cm); and class III (DBH ≥ 30 cm).

Species were classified according to their regeneration, stratification and dispersal strategies. Community dynamics were calculated separately for all pioneer and all non-pioneer species following the classification of Swaine & Whitmore (1988): for understory species, which typically do not reach heights above 15 m; for all canopy species, which typically reach heights above 15 m (Liebsch *et al.* 2008); and for animal-dispersed and non-animal-dispersed species (Ingle 2003). Information about successional, dispersal and dispersal strategies was drawn from the following studies (in alphabetical order, not sorted by relevance): Appolinário *et al.* (2005), Aquino & Barbosa (2009), Araújo *et al.* (2005, 2006), Araujo *et al.* (2010), Brandão *et al.* (2009), Cappelatti & Schmitt (2009), Carvalho *et al.* (2006, 2007), Carvalho & Nascimento (2009), Chagas *et al.* (2001), Colonetti *et al.* (2009), Higuchi *et al.* (2008a), Leite & Rodrigues (2008), Lemos (2008), Lima *et al.* (2010), Lopes *et al.* (2002), Marangon *et al.* (2007), Metzger *et al.* (1997), Norden *et al.* (2009), Nunes *et al.* (2003), Oliveira-Filho *et al.* (2004, 2007), Paula *et al.* (2004), Peixoto *et al.* (2004), Pinto *et al.* (2005), Rolim *et al.* (1999), Silva *et al.* (2004), Stranghetti *et al.* (2003), and Yamamoto *et al.* (2007). In cases of contradictory information, species were allocated to the strategy indicated in the greatest number of references. Community dynamics were calculated separately for common species (≤ 9 individuals) and uncommon species (≥ 10 individuals).

Results

Plot census history

Overall, the number of individuals increased in our plot within the SNF. However, of the 224 species surveyed in 2001, only 214 remained in 2010. Both changes were less than significant (p=0.89 and p=0.81 for the number of individuals and number of species, respectively). Within the community examined, only four new species were recruited between the two censuses (Table 1). Although this net loss of six species reduced the z slope of the species-area relationship (Fig. 1), the differences were not significant (z=0.545 ± 0.032 in 2001 and z=0.531 ± 0.030 in 2010). The various diversity indices indicated an insignificant loss of tree diversity within the plot (Table 2). The basal area increased (from 37.86 m^2 ha^{-1} in 2001 to 40.16 m^2 ha^{-1} in 2010), albeit insignificantly (p=0.44).

Table 1. Tree species with a diameter at breast height of > 3.2 cm and their ecological guilds identified in two censuses of the tree community in a one-hectare plot within a patch of species-rich old-growth forest (Seu Nico Forest, Viçosa, Brazil).

FAMILY Species	2001 (n = 224)	2010 (n = 218)	Ecological guild
ACHARIACEAE			
Carpotroche brasiliensis (Raddi) Endl.	x	x	npio/zoo/us
ANACARDIACEAE			
Astronium fraxinifolium Schott	x	x	npio/nzoo/us
Astronium graveolens Jacq.	x	x	npio/nzoo/cp
Tapirira guianensis Aubl.	x	x	npio/zoo/us
Tapirira obtusa (Benth.) J.D. Mitch.	x	x	npio/zoo/cp
ANNONACEAE			
Annona cacans Warm.	x	x	npio/zoo/cp
Annona neolaurifolia H. Rainer	x	x	npio/zoo/cp
Guatteria australis A. St.-Hil.	x	x	npio/zoo/us
Guatteria villosissima Saint-Hilaire	x	x	npio/zoo/us
Guatteria sp.1	x	x	-/zoo/-
Guatteria sp. 2	x	x	-/zoo/-
Xylopia brasiliensis Spreng.	x	x	npio/zoo/cp
Xylopia sericea A. St.-Hil.	x	x	pio/zoo/us

Continues

Table 1. Continuation.

FAMILY Species	2001 (n = 224)	2010 (n = 218)	Ecological guild
APOCYNACEAE			
Aspidosperma olivaceum Müll. Arg.	x	x	npio/nzoo/us
Aspidosperma polyneuron Müll. Arg.	x	x	npio/nzoo/us
Aspidosperma subincanum Mart.	x	x	npio/nzoo/us
Himatanthus phagedaenicus (Mart.) Woodson	x		npio/nzoo/-
Tabernaemontana hystrix Steud.	x	x	pio/zoo/us
AQUIFOLIACEAE			
Ilex cerasifolia Reissek	x	x	npio/zoo/us
ARALIACEAE			
Dendropanax cuneatus (DC.) Decne. & Planch.	x	x	npio/zoo/sb
Schefflera morototoni (Aubl.) Maguire *et al.*	x	x	pio/zoo/cp
ARECACEAE			
Astrocaryum aculeatissimum (Schott) Burret	x	x	npio/zoo/us
Euterpe edulis Mart.	x	x	npio/zoo/us
Syagrus romanzoffiana (Cham.) Glassman	x		npio/zoo/cp
ASTERACEAE			
Vernonanthura diffusa (Less.) H.Rob.	x	x	pio/nzoo/cp
BIGNONIACEAE			
Handroanthus chrysotrichus (Mart. ex A. DC.) Mattos	x	x	npio/nzoo/us
Jacaranda macrantha Cham.	x	x	npio/nzoo/cp
Sparattosperma leucanthum (Vell.) K. Schum.	x	x	npio/nzoo/us
BURSERACEAE			
Protium heptaphyllum (Aubl.) Marchand	x	x	npio/zoo/cp
Protium warmingianum Marchand	x	x	npio/zoo/cp
Trattinnickia ferruginea Kuhlm.	x	x	-/zoo/cp
CANNABACEAE			
Celtis iguanaea (Jacq.) Sarg.		x	pio/zoo/us
CARDIOPTERIDACEAE			
Citronella paniculata (Mart.) R.A. Howard	x	x	npio/zoo/us
CARICACEAE			
Jacaratia cf. *heptaphylla* (Vell.) A. DC.	x	x	npio/zoo/us
Jacaratia spinosa (Aubl.) A. DC.	x		npio/zoo/cp
CELASTRACEAE			
Maytenus floribunda Reissek	x	x	npio/zoo/us
Maytenus robusta Reissek	x	x	npio/zoo/us
Maytenus salicifolia Reissek	x	x	npio/zoo/us
Salacia elliptica (Mart. ex Schult.) G. Don	x	x	npio/zoo/us
CHRYSOBALANACEAE			
Hirtella hebeclada Moric. *ex* DC.	x	x	npio/zoo/cp
Licania belemii Prance	x	x	-/zoo/cp
CLUSIACEAE			
Kielmeyera albopunctata Saddi	x	x	-/-/cp
Garcinia brasiliensis Mart.	x	x	npio/zoo/us

Continues

Table 1. Continuation.

FAMILY Species	2001 (n = 224)	2010 (n = 218)	Ecological guild
Tovomita glazioviana Engl.	x	x	npio/zoo/cp
Tovomitopsis saldanhae Engl.	x	x	npio/zoo/cp
COMBRETACEAE			
Terminalia glabrascens Mart.	x	x	npio/nzoo/us
CORDIACEAE			
Cordia sellowiana Cham.	x	x	npio/zoo/cp
ELAEOCARPACEAE			
Sloanea hirsuta (Schott) Planch ex Benth.	x	x	npio/zoo/us
ERYTHROXYLACEAE			
Erythroxylum daphnites Mart.	x	x	-/zoo/us
Erythroxylum pelleterianum A. St.-Hil.	x	x	npio/zoo/us
EUPHORBIACEAE			
Alchornea glandulosa Poepp. & Endl.	x	x	pio/zoo/cp
Alchornea triplinervia (Spreng.) Müll. Arg.	x	x	npio/zoo/cp
Aparisthmium cordatum (A.Juss.) Baill.	x	x	npio/nzoo/us
Croton floribundus Spreng.	x	x	pio/nzoo/cp
Croton hemiargyreus Müll. Arg.	x		/////
Mabea fistulifera Mart.	x	x	pio/nzoo/cp
Maprounea guianensis Aubl.	x	x	npio/nzoo/cp
Sapium glandulosum (L.) Morong	x	x	pio/zoo/cp
Euphorbiaceae sp.1	x	x	-/-/-
Euphorbiaceae sp.2	x	x	-/-/-
Euphorbiaceae sp.3	x	x	-/-/-
FABACEAE			
Andira fraxinifolia Benth.	x	x	npio/zoo/us
Apuleia leiocarpa (Vogel) J.F. Macbr.	x	x	npio/nzoo/cp
Caesalpinaceae sp.	x	x	-/-/-
Copaifera langsdorffii Desf.	x	x	npio/zoo/cp
Dalbergia nigra (Vell.) Allemao ex Benth.	x	x	npio/nzoo/cp
Hymenaea sp.	x	x	-/-/-
Inga capitata Desv.	x	x	npio/zoo/cp
Inga cylindrica (Vell.) Mart.	x	x	npio/zoo/cp
Inga vera Willd.	x	x	npio/zoo/cp
Inga sp.1	x	x	-/zoo/cp
Inga sp. 2	x		-/-/-
Lonchocarpus cultratus (Vell.) A.M.G. Azevedo & H.C. Lima	x	x	npio/nzoo/cp
Machaerium caratinganum Kuhlm. & Hoehne	x	x	npio/nzoo//
Machaerium nyctitans (Vell.) Benth.	x	x	npio/nzoo/cp
Machaerium sp.	x	x	-/nzoo/-
Melanoxylon brauna Schott	x	x	npio/nzoo/cp
Moldenhawera sp.	x		-/-/-
Ormosia arborea (Vell.) Harms	x	x	npio/zoo/cp
Peltophorum dubium (Spreng.) Taub.	x	x	npio/zoo/cp

Continues

Table 1. Continuation.

FAMILY Species	2001 (n = 224)	2010 (n = 218)	Ecological guild
Piptadenia gonoacantha (Mart.) J.F. Macbr.	x	x	pio/nzoo/cp
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima	x	x	npio/nzoo/cp
Swartzia acutifolia Vogel	x	x	npio/zoo/cp
Swartzia myrtifolia Sm.	x	x	npio/zoo/us
HUMIRIACEAE			
Vantanea obovata (Nees & Mart.) Benth.		x	-/zoo/us
LACISTEMACEAE			
Lacistema pubescens Mart.	x	x	npio/zoo/us
LAURACEAE			
Aniba firmula (Nees & C. Mart.) Mez	x	x	npio/zoo/cp
Cinnamomum glaziovii (Mez) Kosterm.	x	x	npio/zoo/cp
Cryptocarya moschata Nees & C. Mart. ex Nees	x	x	npio/zoo/cp
Nectandra lanceolata Nees & Mart.	x	x	npio/zoo/cp
Nectandra oppositifolia Nees	x	x	npio/zoo/cp
Ocotea corymbosa (Meisn.) Mez	x	x	npio/zoo/cp
Ocotea dispersa (Nees) Mez	x	x	npio/zoo/us
Ocotea odorifera (Vell.) Rohwer	x	x	npio/zoo/cp
Ocotea pulchella (Nees & Mart.) Mez	x	x	npio/zoo/us
Ocotea silvestris Vattimo-Gil	x	x	npio/zoo/us
Ocotea sp.	x	x	-/zoo/-
Persea wildenowii Kosterm.	x		npio/zoo/cp
Phyllostemonodaphne geminiflora (Mez) Kosterm.	x	x	npio/zoo/us
Urbanodendron verrucosum (Nees) Mez	x	x	npio/zoo/us
Lauraceae sp.1	x	x	-/-/-
Lauraceae sp.2	x	x	-/-/-
Lauraceae sp.3	x		-/-/-
LECYTHIDACEAE			
Cariniana estrellensis (Raddi) Kuntze	x	x	npio/nzoo/cp
Cariniana legalis (Mart.) Kuntze	x	x	npio/nzoo/cp
LYTHRACEAE			
Lafoensia glyptocarpa Koehne	x	x	npio/-/cp
MALVACEAE			
Ceiba speciosa (A. St.-Hil.) Ravenna	x	x	npio/nzoo/cp
Eriotheca candolleana (K. Schum.) A. Robyns	x	x	npio/nzoo/us
Luehea grandiflora Mart. & Zucc.	x	x	npio/nzoo/us
Sterculia curiosa (Vell.) Taroda	x	x	npio/zoo/cp
MELASTOMATACEAE			
Miconia brunnea DC.	x	x	-/zoo/us
Miconia budlejoides Triana	x	x	npio/zoo/us
Miconia cinnamomifolia (DC.) Naudin	x	x	pio/zoo/us
Miconia minutiflora (Bonpl.) DC.	x	x	-/zoo/cp
Miconia tristis Spring	x	x	npio/zoo/us
Mouriri glazioviana Cogn.	x	x	npio/zoo/us

Continues

Table 1. Continuation.

FAMILY Species	2001 (n = 224)	2010 (n = 218)	Ecological guild
MELIACEAE			
Cabralea canjerana (Vell.) Mart.	x	x	npio/zoo/cp
Cedrela fissilis Vell.	x	x	npio/zoo/cp
Guarea fistulosa W. Palacios	x	x	-/zoo/cp
Guarea guidonia (L.) Sleumer	x	x	npio/zoo/cp
Guarea macrophylla Vahl	x	x	npio/zoo/cp
Guarea pendula R.da Silva Ramalho, A.L. Pinheiro & T.D. Penn.	x	x	npio/zoo/us
Trichilia catigua A. Juss.	x	x	npio/zoo/us
Trichilia emarginata (Turcz.) C. DC.	x	x	npio/zoo/us
Trichilia lepidota Mart.	x	x	npio/zoo/cp
Trichilia pallida Sw.	x	x	npio/zoo/cp
MONIMIACEAE			
Mollinedia schottiana (Spreng.) Perkins	x	x	npio/zoo/us
Monimiaceae sp.	x		-/-/-
MORACEAE			
Clarisia ilicifolia (Spreng.) Lanj. & Rossberg	x	x	npio/zoo/us
Brosimum guianense (Aubl.) Huber	x	x	npio/zoo/cp
Ficus gomelleira Kunth & C.D. Bouché	x	x	npio/zoo/cp
Ficus luschnathiana (Miq.) Miq.	x	x	npio/zoo/cp
Ficus enormis Mart. *ex* Miq.	x	x	npio/zoo/cp
Helicostylis tomentosa (Poepp. & Endl.) Rusby	x	x	npio/zoo/cp
Maclura tinctoria (L.) D. Don ex Steud.	x	x	npio/zoo/cp
Naucleopsis oblongifolia (Kuhlm.) Carauta	x	x	npio/zoo/cp
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. & Wess. Boer	x	x	npio/zoo/us
Sorocea hilariana Gaudich.	x	x	Npio/zoo/us
MYRISTICACEAE			
Virola bicuhyba (Schott *ex*. Spreng.) Warb.	x	x	npio/zoo/cp
Virola gardneri (A. DC.) Warb.	x	x	npio/zoo/cp
MYRTACEAE			
Calyptranthes brasiliensis Spreng.	x	x	npio/zoo/us
Campomanesia xanthocarpa (Mart.) O. Berg	x	x	npio/zoo/us
Eugenia cf. *lambertiana* DC.	x	x	npio/zoo/us
Eugenia dodonaeifolia Cambess.	x	x	npio/zoo/us
Eugenia florida DC.	x	x	npio/zoo/us
Eugenia leptoclada O.Berg	x	x	npio/zoo/us
Marlierea excoriata Mart.	x	x	npio/zoo/us
Marlierea suaveolens Cambess.	x	x	npio/zoo/us
Marlierea cf. *teuscheriana* (O.Berg) D.Legrand	x	x	npio/zoo/us
Myrcia anceps (Spreng.) O. Berg	x	x	npio/zoo/us
Myrciaria floribunda (H.West ex Willd.) O.Berg	x	x	npio/zoo/us
Myrcia pallida (Cambess.) O. Berg	x	x	npio/zoo/-
Myrcia pubipetala Miq.	x	x	npio/zoo/us
Myrcia splendens (Sw.) DC.	x	x	npio/zoo/us
Myrcia sp.	x	x	-/zoo/-
Neomitranthes sp.	x	x	-/zoo/us
Plinia cf. *grandifolia* (Mattos) Sobral	x	x	npio/zoo/us
Psidium cf. *oblongatum* O. Berg	x	x	-/zoo/-
Myrtaceae sp.	x	x	-/zoo/-

Continues

Table 1. Continuation.

FAMILY Species	2001 (n = 224)	2010 (n = 218)	Ecological guild
NYCTAGINACEAE			
Guapira hirsuta (Choisy) Lundell	x	x	npio/zoo/us
Guapira opposita (Vell.) Reitz	x	x	npio/zoo/us
Pisonia ambigua Griseb.	x	x	npio/zoo/cp
Nyctaginaceae sp.	x	x	-/zoo/-
OCHNACEAE			
Ouratea polygyna Engl.	x	x	npio/zoo/us
OLACACEAE			
Heisteria silvianii Schwacke	x	x	npio/zoo/us
Tetrastylidium grandiflorum (Baill.) Sleumer	x	x	npio/zoo/us
Oleaceae sp.	x	x	-/zoo/-
PERACEAE			
Pera glabrata (Schott) Poepp. ex Baill.	x	x	npio/zoo/cp
PHYLLANTHACEAE			
Hieronyma alchorneoides Allemão	x	x	npio/zoo/cp
Margaritaria nobilis L. f.	x	x	npio/zoo/cp
PIPERACEAE			
Piper arboreum Aubl.	x	x	npio/zoo/us
Piper gigantifolium C. DC.	x	x	-/zoo/us
PRIMULACEAE			
Cybianthus fuscus Mart.		x	-/zoo/-
Myrsine umbellata Mart.	x	x	npio/zoo/us
Stylogyne pauciflora (Mart. & Miq.) Mez	x	x	-/zoo/us
RHAMNACEAE			
Colubrina glandulosa Perkins	x	x	npio/zoo/cp
ROSACEAE			
Prunus myrtifolia (L.) Urb.	x	x	npio/zoo/cp
RUBIACEAE			
Alseis floribunda Schott	x	x	npio/zoo/us
Amaioua guianensis Aubl.	x	x	npio/zoo/us
Bathysa cuspidata (St. Hil.) Hook.f. *ex* K.Schum.	x	x	npio/aut/us
Bathysa nicholsonii K. Schum.	x	x	npio/aut/us
Genipa americana L.	x	x	npio/zoo/cp
Guettarda viburnoides Cham. & Schltdl.	x	x	npio/zoo/us
Ixora gardneriana Benth.	x	x	npio/zoo/us
Psychotria carthagenensis Jacq.	x	x	npio/zoo/us
Psychotria rhytidocarpa Müll. Arg.	x	x	npio/zoo/us
Psychoria myriantha Müll. Arg.	x	x	npio/zoo/us
Psychotria nuda (Cham. & Schltdl.) Wawra	x	x	npio/zoo/us
Psychotria vellosiana Benth.	x	x	npio/zoo/us
Psychotria sp.	x	x	-/zoo/-
Randia ferox (Cham. & Schltdl.) DC.	x	x	npio/zoo/us
Rudgea jasminoides (Cham.) Müll.Arg.	x	x	npio/zoo/us
Rubiaceae sp.		x	-/zoo/-
RUTACEAE			
Hortia brasiliana Vand. ex DC.	x	x	-/zoo/cp
Zanthoxylum rhoifolium Lam.	x	x	npio/zoo/us

Continues

Table 1. Continuation.

FAMILY Species	2001 (n = 224)	2010 (n = 218)	Ecological guild
SABIACEAE			
Meliosma itatiaiae Urb.	x	x	-/zoo/us
SALICACEAE			
Casearia arborea (Rich.) Urb.	x	x	npio/zoo/cp
Casearia decandra Jacq.	x	x	npio/zoo/cp
Casearia gossypiosperma Briq.	x	x	npio/nzoo/us
Casearia sylvestris Sw.	x	x	pio/zoo/us
Casearia ulmifolia Vahl ex Vent.	x	x	npio/zoo/us
Macrothumia kuhlmannii (Sleumer) M.H.Alford	x	x	-/zoo/cp
Prockia crucis P. Browne ex L.	x	x	npio/zoo/us
Xylosma prockia (Turcz.) Turcz.	x	x	npio/zoo/us
Salicaceae sp.	x	x	-/zoo/-
SAPINDACEAE			
Allophylus edulis (A. St.-Hil. *et al.*) Hieron. ex Niederl.	x	x	npio/zoo/us
Cupania vernalis Cambess.	x	x	npio/zoo/cp
Matayba elaeagnoides Radlk.	x	x	npio/zoo/cp
SAPOTACEAE			
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	x	x	npio/zoo/cp
Chrysophyllum lucentifolium Cronquist	x	x	npio/zoo/us
Chrysophyllum cf. *marginatum* (Hook. & Arn.) Radlk.	x	x	npio/zoo/cp
Chrysophyllum sp.	x	x	-/zoo/-
Pouteria caimito (Ruiz & Pav.) Radlk.	x	x	npio/zoo/cp
Pradosia lactescens (Vell.) Radlk.	x	x	npio/zoo/cp
SIPARUNACEAE			
Siparuna guianensis Aubl.	x	x	npio/zoo/us
Siparuna reginae (Tul.) A. DC.	x	x	npio/zoo/us
SOLANACEAE			
Brunfelsia uniflora (Pohl) D. Don	x	x	npio/zoo/us
Cestrum mariqitense Kunth	x	x	-/zoo/us
Cestrum sp.	x	x	-/zoo/-
Solanaceae sp.	x	x	-/zoo/-
URTICACEAE			
Cecropia hololeuca Miq.	x	x	pio/zoo/cp
Coussapoa floccosa Akkermans & C.C. Berg	x	x	-/zoo/us
Coussapoa microcarpa (Schott) Rizzini	x	x	npio/zoo/cp
Pourouma guianensis Aubl.	x	x	pio/zoo/cp
VOCHYSIACEAE			
Qualea multiflora Mart.	x	x	npio/zoo/cp
UNKNOWN FAMILY			
Unidentified sp.1	x	x	-/-/-
Unidentified sp.2	x	x	-/-/-
Unidentified sp.3	x		-/-/-
218 species			

pio – pioneer; npio – non-pioneer; zoo – zoochorous (animal-dispersed); nzoo – non-zoochorous (non-animal-dispersed); us – understory; cp – canopy.

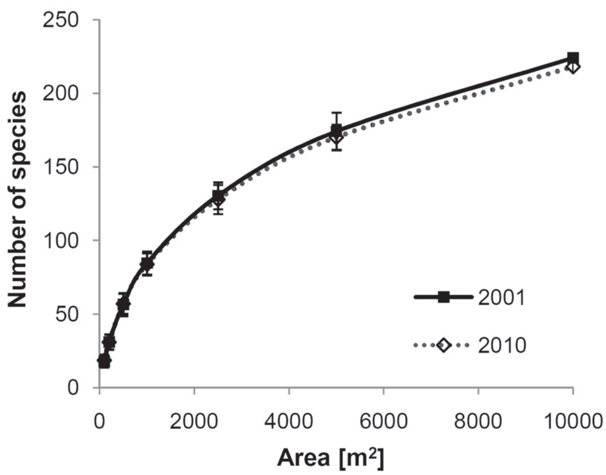

Figure 1. Rarefaction of the species accumulation curves for censuses conducted in 2001 and 2010 in a one-hectare plot within a patch of species-rich old-growth forest (Seu Nico Forest, Viçosa, Brazil). Species-area relationship, fitted by the power model, does not differ significantly between 2001 and 2010, in terms of the log number of species (0.545 ± 0.032 vs. 0.531 ± 0.030) or the log area (+0.233 ± 0.099 vs. +0.273 ± 0.093).

Table 2. Changes in tree species diversity between two censuses, conducted nine years apart, in a one-hectare plot within a patch of species-rich old-growth forest (Seu Nico Forest, Viçosa, Brazil).

Diversity index	2001	2010	p*
Fisher's alpha	59.69 ±2.25	57.2 ± 2.17	0.27
Shannon-Wiener	4.42	4.37	0.86
Simpson	43.08	39.87	0.71

*Two-sample t-test.

Community dynamics

Between the first and second censuses, the number of individuals increased because recruitment exceeded mortality (Table 3). In terms of basal area, gains surpassed losses, resulting in a net gain from 2001 to 2010. Among the common species, mortality and recruitment rates were nearly identical. However, among the uncommon species, the mortality rate was higher than was the recruitment rate. In comparison with that observed for the community as a whole, mortality was disproportionately high among the pioneer and non-animal dispersed species. Among the understory species, recruitment exceeded mortality.

Population dynamics

Of the nine species that were the most abundant in 2001, eight increased in abundance, only *Bathysa nicholsonii* being less represented in 2010 than in 2001 (Table 4). Of the 20 species with the highest basal areas, 10 increased their basal area by more than 10%. In five species, there was a moderate to high increase in basal area, which decreased in another five species.

Species ranks from both censuses showed an s-shaped curve (Fig. 2). Due to lower species richness and higher abundance of common species in 2010, the curve trended downward, although the slope decreased only slightly from 2001 to 2010 (from −0.0089 ± 0.0009 to −0.0083 ± 0.0008).

Mortality rates were high for some of the uncommon species, such as *Vernonanthura diffusa* (15.4% yr^{-1}) and *Astronium fraxinifolium* (13.1% yr^{-1}), whose populations declined. The populations of other species increased considerably, with above-average recruitment rates. Examples are *Siparuna reginae* (23.1% yr^{-1}) or *Eugenia florida* (13.4% yr^{-1}). Among the most abundant species, recruitment rates were above average for *Siparuna guianensis* (3.1% yr^{-1}), *Euterpe edulis* (4.1% yr^{-1}), *Virola gardneri* (3.3% yr^{-1}) and *Eugenia* cf. *lambertiana* (3.9% yr^{-1}), whereas mortality rates were above average for *Bathysa nicholsonii* (2.6% yr^{-1}), *S. guianensis* (2.4% yr^{-1}), *Pourouma guianensis* and (2.5% yr^{-1}) and *Casearia ulmifolia* (2.4% yr^{-1}).

Discussion

Within the 1 ha plot of the SNF evaluated, we obtained low values for the key features of community dynamics, such as recruitment, mortality and growth rates, as well as losses and gains of basal area (Leigh *et al.* 2004; Thompson *et al.* 2004). Within the Atlantic Forest and the Cerrado domains, mortality and recruitment rates are generally higher for flooded gallery forests (Lopes & Schiavini 2007; Higuchi *et al.* 2008b; Fontes & Walter 2011) than for non--flooded gallery forests (Pinto 2002; Oliveira-Filho & Felfili 2008), for seasonal deciduous forests (Carvalho & Felfili, 2011), for seasonal semideciduous forests (Apollinario *et al.* 2005; Oliveira-Filho *et al.* 1997, 2007; Silva & Araújo 2009; Machado & Oliveira-Filho 2010) and for evergreen forests (Rolim *et al.* 1999; Saiter *et al.* 2011).

The mortality and recruitment rates reported in the literature are higher than those observed for our study site, indicating that there was high stability in the SNF. This stability is congruent with the findings reported by Saiter *et al.* (2011) for other old-growth, mature forests.

For the SNF plot evaluated, size class was not found to correlate with mortality or recruitment. In disturbed forests, mortality is typically higher among the smaller size classes usually because of the effect known as self-thinning (Oliveira-Filho *et al.* 2007; Saiter *et al.* 2011). However, the observations that mortality exceeded recruitment among pioneer species and recruitment exceeded mortality among animal-dispersed species, as well as among understory species, indicates a slight successional advance of the SNF as a mature forest, making it even more representative of an old-growth forest (Liebsch *et al.* 2008).

Turnover rates were high only for some of the uncommon species (data not shown). Due to a low number of individuals, even small alterations within these populations result in high rates. Among the twenty most abundant

Table 3. Tree demographic dynamics in two censuses, conducted nine years apart (in 2001 and 2010), in a one-hectare plot within a patch of species-rich old-growth forest (Seu Nico Forest, Viçosa, Brazil).

Category	Growth	Mortality	Recruitment	Basal area	
				Lost	Gained
	(mm yr^{-1})	(% yr^{-1})	(% yr^{-1})	(m^2 ha^{-1} yr^{-1})	(m^2 ha^{-1} yr^{-1})
All	1.12	1.65	1.84	0.47	0.73
Size class (cm DBH)					
3.2-9.9	0.81	1.88	2.69	0.79	0.15
10-29.9	1.79	0.98	2.07	0.15	0.32
≥30	2.10	1.75	2.48	0.24	0.26
Abundance class*					
Uncommon (≤ 9 species)	1.31	2.09	1.78	0.18	0.22
Common (≥ 10 species)	1.08	1.54	1.56	0.29	0.51
Successional group					
Pioneer	1.56	3.37	1.74	0.09	0.04
Non-pioneer	1.11	1.59	1.84	0.39	0.69
Disperal group					
Animal-dispersed	0.62	1.48	1.73	0.34	0.59
Non-animal-dispersed	1.24	2.86	0.61	0.13	0.12
Vertical position					
Understory	0.49	1.73	3.53	0.14	0.33
Canopy	0.91	1.44	0.99	0.32	0.39

DBH – diameter at breast height.
*Refers to the 2001 census.

species, turnover rates were above average for only a few, including *S. guianensis*, *E. edulis*, *V. gardneri*, and *E.* cf. *lambertiana*, which are non-pioneer, animal-dispersed species, the occurrence of which indicates forest maturation (Liebsch *et al.* 2008). Several of the most abundant species showed high mortality rates, the highest being for *P. guianensis*. Because *P. guianensis* is a pioneer species, a decline in its population is also indicative of the ongoing successional change in the SNF.

Although the recruitment and mortality rates, as well as the gains and losses of basal area, indicate stability and slight successional advance for the tree community of the SNF, our comparison of the two censuses revealed some tendencies that merit discussion. As species richness and diversity declined, common species became more common, while rare species became rarer. In addition, the number of individuals and the total basal area both increased. The fact that those tendencies were not significant might be due to the small sample size. However, it is also possible that they were stochastic, describing only the natural oscillations within the dynamic equilibrium of the seasonal semideciduous Atlantic Forest (Rees *et al.* 2001; Lopes & Schiavini 2007; Paiva *et al.* 2007). Nevertheless, an increase in the number of individuals contradicts the zero-sum assumptions made by Hubbell in a theoretical work (2001). In addition, because the amount of biomass supported within an ecosystem depends on energy and resource inputs (Ernest *et al.* 2009), the increase in basal area might be explained by increased resource availability (Lewis *et al.* 2004), perhaps due to climate change (IPCC 2007). This is alarming, because the same tendencies have recently been observed in other regions of the Atlantic Forest (Higuchi *et al.* 2008b; Carvalho & Felfili 2011; Saiter *et al.* 2011).

Regarding the decline in species richness, Felfili *et al.* (2000) stressed the difficulty in interpreting what they referred to as "pseudoextinction", because species might still be present within the community in form of seeds, seedlings or treelets that have not yet met the inclusion criterion. However, if a net loss of six species represents a natural oscillation of the tree community, a net gain of six species in nine years, perhaps in the next census or in similar studies, could be expected. We are not aware of any studies reporting such net gains in primary or late secondary forests; on the contrary, most dynamic studies conducted to date have also reported declining numbers of species (Oliveira--Filho *et al.* 1997; Bunyavejchewin *et al.* 2004; Lee *et al.* 2004; Leigh *et al.* 2004; Thompson *et al.* 2004; Werneck & Franceschinelli 2004; Higuchi *et al.* 2008a, 2008b; Machado & Oliveira-Filho 2010).

Table 4. Species ranking, by species abundance (left half) and by basal area (right half), from the second of two censuses conducted in a one-hectare plot within a patch of species-rich old-growth forest (Seu Nico Forest, Viçosa, Brazil).

Rank (2010)	Number of trees					Basal area				
	Species	2001 n	2010 n	Diff.	% of trees (2010)	Species	2001 (m^2 ha^{-1})	2010 (m^2 ha^{-1})	Diff.	% of trees (2010)
1	*Siparuna guianensis* Aubl. (Siparunaceae)	240	254	+	10.04	*Ficus gomelleira* Kunth & C.D. Bouché (Moraceae)	3.097	3.405	++	0.04
2	*Protium warmingiana* March, L. (Burseraceae)	115	121	+	4.784	*Pseudopiptadenia contorta* (DC.) G.P. Lewis & M.P. Lima (Fabaceae)	2.988	3.082	+	1.78
3	*Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. &Wess. Boer (Moraceae)	101	107	+	4.231	*Virola gardneri* (A. DC.) Warb. (Myristicaceae)	1.876	2.221	+++	3.08
4	*Myrciaria floribunda* (H.WestexWilld.) O.Berg (Myrtaceae)	77	101	+++	3.994	*Guatteria nigrescens* Mart. (Annonaceae)	1.709	1.912	+++	2.65
5	*Euterpe edulis* Mart. (Arecaceae)	68	90	+++	3.559	*Sterculia chicha* A. St.-Hil. Ex Turpin (Malvaceae)	1.948	1.840	−−	0.47
6	*Virola gardneri* (A. DC.) Warb. (Myristicaceae)	59	78	+++	3.084	*Ceiba speciosa* (A. St.-Hil.) Ravenna (Malvaceae)	1.301	1.371	++	0.04
7	*Helicostylis tomentosa* (Poepp. &Endl.) Rusby (Moraceae)	72	73	+	2.887	*Protium warmingiana* March, L. (Burseraceae)	1.093	1.292	+++	4.78
8	*Guatteria nigrescens* Mart. (Annonaceae)	65	67	+	2.649	*Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. &Wess. Boer (Moraceae)	1.125	1.258	+++	4.23
9	*Bathysa nicholsonii* K. Schum. (Rubiaceae)	71	60	−−−	2.372	*Astronium graveolens* Jacq. (Anacardiaceae)	1.004	0.974	−	0.51
10	*Marlieria excoriata* Mart. (Myrtaceae)	61	59	−	2.333	*Ocotea silvestris* Vattimo (Lauraceae)	0.647	0.822	+++	0.95
11	*Phyllostemonodaphne geminiflora* (Mez) Kosterm. (Lauraceae)	62	59	−	2.333	*Casearia ulmifolia* Vahl ex Vent. (Salicaceae)	0.682	0.728	++	1.19
12	*Brosimum guianense* (Aubl.) Huber(Moraceae)	48	49	+	1.938	*Pourouma guianensis* Aubl. (Urticaceae)	0.815	0.659	−−−	1.23
13	*Eugenia* cf. *lambertiana* O. Berg (Myrtaceae)	37	47	+++	1.858	*Helicostylis tomentosa* (Poepp. &Endl.) Rusby (Moraceae)	0.552	0.643	+++	2.89
14	*Pseudopiptadenia contorta* (DC.) G.P. Lewis & M.P. Lima (Fabaceae)	56	45	−−	1.779	*Euterpe edulis* Mart. (Arecaceae)	0.507	0.638	+++	3.56
15	*Trichilia emarginata* (Turcz.) C. DC. (Meliaceae)	33	35	+	1.384	*Bathysa nicholsonii* K. Schum. (Rubiaceae)	0.679	0.595	−−−	2.37
16	*Trichilia catigua* A. Juss. (Meliaceae)	36	34	−−	1.344	*Brosimum guianense* (Aubl.) Huber (Moraceae)	0.524	0.594	+++	1.94
17	*Alseis floribunda* (Standl.) Steyerm. (Rubiaceae)	26	31	+++	1.226	*Siparuna guianensis* Aubl. (Siparunaceae)	0.573	0.577	+	10.04
18	*Pourouma guianensis* Aubl. (Urticaceae)	35	31	−−−	1.226	*Guarea macrophylla* Vahl (Meliaceae)	0.592	0.555	−−	0.59
19	*Casearia ulmifolia* Vahl ex Vent. (Salicaceae)	36	30	−−−	1.186	*Virola oleifera* (Schott) A.C. Sm. (Myristicaceae)	0.472	0.554	+++	0.71
20	*Chrysophyllum lucentifolium* Cronquist (Sapindaceae)	27	28	+	1.107	*Ocotea odorífera* Rohwer (Lauraceae)	0.448	0.544	+++	1.07

Diff. – difference; + – moderate increase (< 5%); ++ – considerable increase (5-10%); +++ significant increase (> 10%), − – moderate loss (< 5%); −− – considerable loss (5-10%); −−− – significant loss (> 10%).

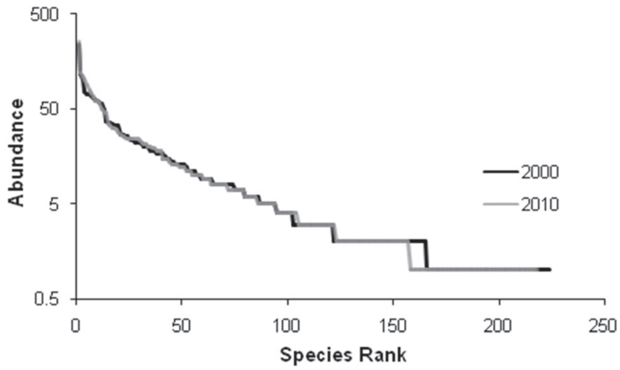

Figure 2. Species rank from censuses conducted in 2001 and 2010 in a one-hectare plot within a patch of species-rich old-growth forest (Seu Nico Forest, Viçosa, Brazil).

Because these observations have been made within a landscape that was logged recently (about 150 years ago) and is now fragmented, they should be discussed from a metacommunity perspective. According to the species-area relationship, one of the most widely studied patterns in ecology (Tjørve 2003; Martin & Goldenfeld 2006; Colwell *et al.* 2012), habitat area loss causes species loss (Pimm & Raven 2000; Ney-Nifle & Mangel 2000; Fischer 2000; He & Hubbell 2011). However, decades of research on species-area relationships have also revealed that species richness is lower on islands than on contiguous land masses of the same area (Rosenzweig 1995; Lomolino 2001). Because landscape fragmentation might be interpreted as the transformation of former contiguous habitats into small patches, forming continental islands, theory predicts that a secondary, delayed loss of species should occur after landscape fragmentation (Rosenzweig 1995).

According to the theory of biogeography, species richness at a given site is achieved by maintaining equilibrium among the rates of immigration, speciation (Hubbell 2001) and extinction (MacArthur & Wilson 1967). In the present study more species disappeared from the community than were recruited. Therefore, we might assume that there was a disturbance of this equilibrium, indicating problems with the immigration of propagules of new species to the SNF. Against this conclusion stands the observation that recruitment rates were higher for animal-dispersed species than for non-animal-dispersed species (Table 3), and that the four new species were animal-dispersed. This indicates that an adapted fauna is actually dispersing seeds and fruits within the fragment and should guarantee genetic exchange between the SNF and neighboring fragments. However, as research activities in the last decades have shown, these secondary fragments are less species-rich (Lopes *et al.* 2002; Meira-Neto & Martins 2002; Paula *et al.* 2004; Ribas *et al.* 2004; Ferreira Jr. *et al.* 2007). This reduces the richness of arriving seeds and therefore the immigration rate of propagules from new species. Nevertheless, natural extinction, in our case measured as pseudoextinction (Felfili *et al.* 2000; Carvalho & Felfili 2011), continues unchanged, which causes ongoing species loss. In this scenario, species loss in the SNF will continue until a new equilibrium is reached between extinction and reduced immigration rate. These theoretical explications of the species loss observed in the SNF are congruent with the findings of Hubbell (2001), who ran simulations of the distribution of species abundance in local communities. In isolated stands (communities with reduced immigration rates), common species become more common and rare species become rarer, as was observed in the SNF plot evaluated here. This is a vicious cycle: due to isolation, common species become more common in the local community but also increase their abundance in the metacommunity. Because abundance in the local community, even in isolation, still depends on species abundance in the metacommunity, this commonness of already common species further increases metacommunity abundance. Increased mortality of uncommon species supports the categorization of the species loss observed in the SNF as time-delayed species loss after landscape fragmentation.

As shown above, our tree community dynamics study of the SNF indicated stability and low dynamics in this unique patch of primary forest. The slight, insignificant decline in species richness and the increase in basal area might be due to natural oscillations around an equilibrium value but might also be interpreted as consequences of environmental changes that are currently affecting vegetation and will do so into the future. Future censuses in the same SNF plot showing similar tendencies will support our hypothesis that the changes observed in this, one of the last old-growth forest remnants in the region, are due to human activity worldwide.

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