Biodivers Conserv (2012) 21:2181–2193
DOI 10.1007/s10531-011-0213-y

ORIGINAL PAPER

Species richness of plants and fungi in western Panama: towards a fungal inventory in the tropics

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Received: 25 August 2011 / Accepted: 8 December 2011 / Published online: 22 December 2011

Abstract In order to document the species richness of plants and fungi in a tropical area, a trail of 500 m in tropical lowlands in the Chiriquí province, on the Pacific side of western Panama, was sampled each month during 2 years with 2 h dedicated to plants and 2 h dedicated to fungi, each by two botanists or mycologists respectively. The 24 sampling events yielded approximately 4,000 records of plants corresponding to 311 species as well as 1,614 records of fungi corresponding to approximately 567 species. Lists of more or less certain names of plants and fungi as well as voucher specimens are provided. The randomized species accumulation curve for plants approaches an asymptote and estimators yield stable values of 310–318 predicted plant species in the area of investigation. The curve for records of fungal species, however, did not saturate and all applied estimator functions failed to predict the total richness of fungi for the area convincingly. Two plant collections correspond to new records for Panama and 54 species and infraspecific taxa are new for the Chiriquí province. The identification of fungi is still in process and yielded two species probably new to science as well as 17 new records of species for Panama to date. In order to assess biodiversity patterns (e.g. fungi to plant ratios) of tropical fungi more

Electronic supplementary material The online version of this article (doi:10.1007/s10531-011-0213-y) contains supplementary material, which is available to authorized users.

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accurately, it is necessary to repeat such investigations in other areas and to improve the tools for taxonomic identification of these highly diverse but mostly microscopic organisms.

Keywords Chiriquí province · Diversity of fungi · Diversity of plants · Estimators · New records · Tropical fungi · Tropical plants · Taxonomic identifications

Introduction

As highly diverse, microscopically abundant and omnipresent organisms, fungi are important in any ecosystem especially for the decomposition of dead organic material, nutrient cycling, vigorous growth of plants (productivity), as well as for biological control of dominant species by parasitic fungi (e.g. Hawksworth 1998). Fungi have to be considered when the resistance and resilience of ecosystems to perturbations by direct human impact or by climate change are discussed (Lilleskov et al. 2002; Van Herk et al. 2002; Lensing and Wise 2006; Gange et al. 2007).

Probably all investigators of fungal diversity agree that it is practically impossible to catalogue all fungi of a given site (e.g. Cannon 1999; Schmit and Lodge 2005) for the following reasons: Most fungi are microscopic organisms—inventories, however, mostly are based on macroscopically evident fruiting bodies; The occurrence of fungal fruiting bodies strongly varies in time (seasonality), depending on moisture, temperature, and other factors (Watling 1995; Rossman et al. 1998); Many fruiting bodies of fungi are ephemeral; Numerous opportunistic fungi are dispersed by spores and spontaneously occur anywhere at any time given favorable environmental conditions and suitable substrates; Fungi are hyperdiverse, a fact particularly evident by results obtained by environmental sequencing (Buée et al. 2009; Hibbett et al. 2011).

Some areas have been surveyed for many years, with lists of fungal species still increasing in size with every further effort. Some of the most impressive examples are listed in Table 1. These fungal surveys are located in areas with a temperate climate and are mostly focused on the fruiting bodies of macrofungi. Hawksworth (1991) calculated a ratio of species of plants to species of fungi in a given area of approximately 1:6 based on numbers of plants and fungi known for the British Isles, numbers of fungal species associated with particular plant species, and the ratios in some well-studied sites. He presented a global estimation of 1.5 million existing species of fungi (Hawksworth 1991, 2001). The ratio might be used at different scales and in different parts of the world, but we do not know whether it is constant when applied to areas of different sizes, with a different diversity of the plant community, climate, and environmental factors (Mueller and Schmit 2007). We urgently need data on the relation of species numbers of plants to fungi for comparison, especially from tropical areas (e.g. Watling 1995; Hawksworth 2001).

No complete inventory exists for a tropical region, but some studies aim towards fungal inventories in tropical areas (Hawksworth 1997). Some checklists of fungi reported for different tropical countries or areas as well as ecological studies focusing on certain niches, such as tissue of leaves (endophytes), ecological aspects, methodology of diversity assessment, and/or selected groups of fungi are available (e.g. Arnold et al. 2000; Buée et al. 2009; Cantrell 2004; Guevara and Dirzo 1998; Haug et al. 2010; Hibbett et al. 2011; Hyde et al. 2007; Jumpponen and Jones 2009; Lodge and Cantrell 1995b). Therefore, some aspects of fungal communities and factors important for their diversity are known for tropical forests (reviewed by Lodge and Cantrell 1995a). As taxonomic identification is

Table 1 Examples of sites investigated for fungi over long periods of time

Country	Area	Size	Investigated	Number of known species of fungi	References
England	Esher Common, Surrey	ca. 400 ha	During at least 25 years	>2,900	Cannon et al. (2001)
England	Slapton National Nature Reserve, Devon	208 ha	Since 1969	>2,500	Hawksworth (1997); Cannon et al. (2001)
Germany	Mecklenburg–Western Pomerania	ca. 2,318,000 ha	During more than 50 years	>3,000	Unterseher et al. (2011b)
Scotland	Dawyck Botanic Garden	25 ha	During more than 15 years	Almost 1,000	Watling (2010)
Germany	Extensively farmed pasture in Fünfseenland, Bavaria	ca. 3.8 ha	Since 1996	Almost 1,000	Karasch (2005)

difficult, however, in ecological studies names might be neglected, so they are useless for analyses of beta diversity, e.g. the comparison of diversity of different sampling sites and times. Only few studies include lists of species and specimens (e.g. Chaverri and Vílchez 2006; Guevara and Dirzo 1998; Pérez and Camino 2000). A proposal for an all fungal taxa inventory for a conservation area in Costa Rica by Rossman et al. (1998) demonstrates the enormous effort necessary for a complete inventory—a project which unfortunately has never been realized.

Notwithstanding, exhaustive and vouchered sampling is necessary for subsequent estimations and extrapolations of species richness and comparison of communities (e.g. Coddington et al. 2009). If too many species are missing or rarely recorded, extrapolation of species richness beyond observed values is critical because of important statistical errors (Chao et al. 2009; O'Hara 2005). If undersampling is a salient feature of biodiversity studies, then pseudovariability may be observed between different places or times, which may lead to incorrect interpretation of the results. Great progress has been made in this field of science during the last two decades (Chao 1987 and others reviewed in Colwell and Coddington 1994 and O'Hara 2005), and tools originally designed for macroorganisms have been adopted for the analysis of microorganisms (Bohannan and Hughes 2003; Pedrós-Alió 2006; Unterseher et al. 2008, 2011a).

Taxonomic identifications are essential to integrate new knowledge on species diversity of a given site into the huge body of knowledge existing on the geographical distribution, morphology, ecology, and evolution of fungi (e.g. Schmit and Lodge 2005). Especially in the context of fungal all taxa inventories, the quality of the identifications might be low, as they are done by non-specialists. Therefore, voucher material is very important, so that the records are of long-term value (Hawksworth 2004; Hawksworth and Mueller 2005).

The present study is an attempt to test the Hawksworth hypothesis of a 1:6 fungus plant ratio for a tropical region. It is unique in that it was realized in the tropics during 2 years with monthly sampling, all taxa of directly visible fungi and vascular plants are considered, more or less tentative taxonomic identifications are presented, and voucher specimens will be provided. Apart from a study on microfungi in Tanzania by Pirozynski (1972), a similar undertaking has not been reported.

Materials and methods

From casual visits to the area later chosen for the present analysis (Fig. 1a, b), we noticed that fungi visible with the naked eye were different at every visit. In the context of the project "Plant Parasitic Microfungi in Western Panama" (Mangelsdorff et al. this issue; Piepenbring et al. 2011) we learnt that numerous visits to the same area would be necessary in order to work towards an inventory. According to Cantrell (2004) at least 12 sampling events per year should be realized when the aim is an all taxa inventory. Taking into consideration time and human resources available for the present study, the following sampling strategy was established.

At monthly intervals from Feb 2009 to Jan 2011, two experienced botanists/mycologists spent 2 h for the investigation of plants and 2 h for the investigation of fungi on a trail of 500 m in secondary lowland vegetation in western Panama. When two experienced persons were not available, the work was performed by one professional and at least two less experienced people (students) or during a longer period of time, in compensation.

The trail is located in western Panama, Prov. Chiriquí, Corregimiento Dolega, north of David, between the small town Los Algarrobos and the Majagua river, between N 08°

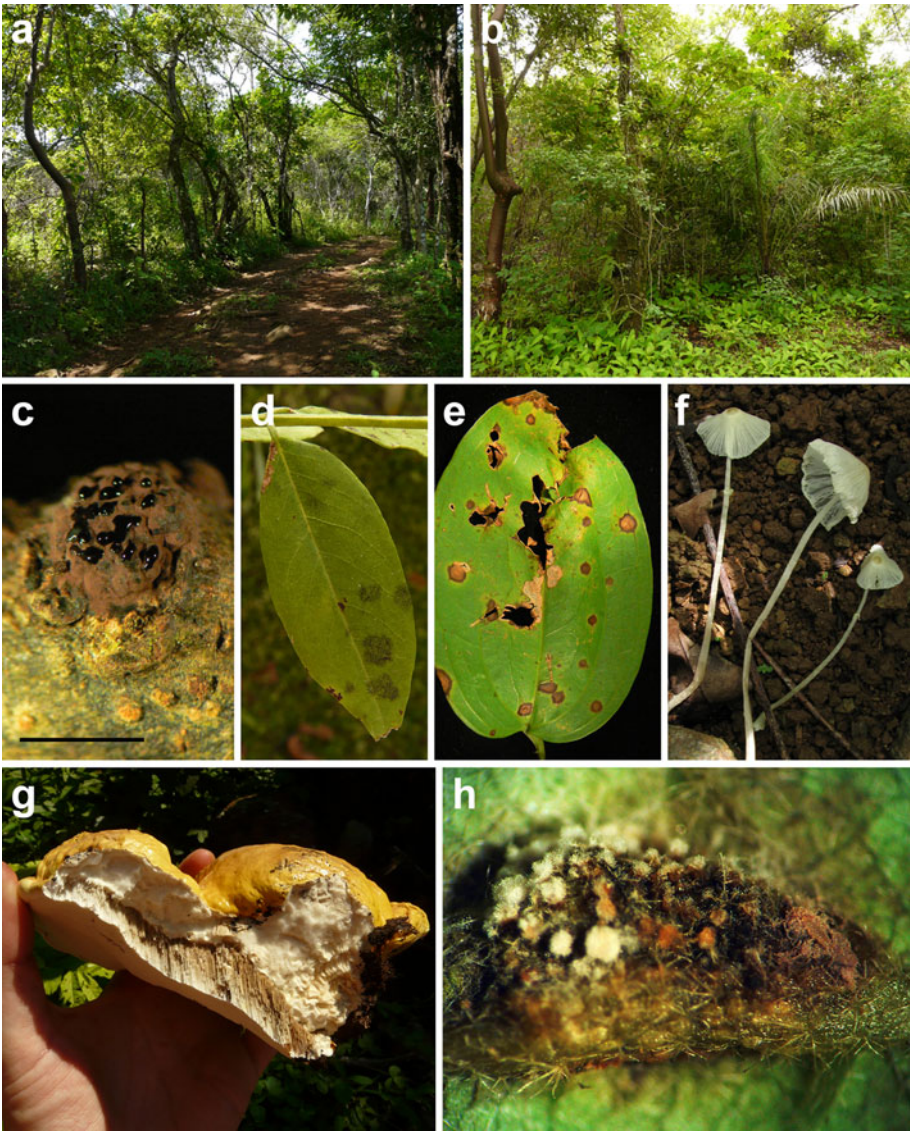

Fig. 1 The site of the investigation located in western Panama, and fungi representing important systematic groups. **a** The trail with bordering trees and rural vegetation. **b** The border of the secondary forest. **c** *Hypoxylon pelliculosum* (*Xylariales*, *Ascomycota*) with ascospores libertated in liquid drops (M 677). *Scale bar* = 2 mm. **d** Colonies of *Meliola bicornis* (*Meliolales*, *Ascomycota*) on a leaflet of *Gliricidia sepium* (M 774). **e** Lesions caused by *Cercospora smilacis* (asexual fungus) on a leaf of *Smilax* sp. (M 495). **f** *Leucocoprinus fragilissimus* (*Agaricales*, *Basidiomycota*) (M 955). **g** *Ganoderma colossum* (*Polyporales*, *Basidiomycota*) (M 285). **h** Sori of *Pucciniosira dorata* (*Pucciniales*, *Basidiomycota*) on a gall (a few millimetres long) formed by leaf tissue of *Triumfetta* cf. *lappula* (M 695). Note the presence of white hyphae and conidia of *Acremonium* sp. (asexual fungus) on the left hand side and violet spore mass of *Tuberculina* sp. (asexual fungus) eaten by a larva of *Cecidomyiidae* on the right hand side

29,47 W 082° 25,92 and N 08° 29,17 W 082° 26,03, at 120–150 m a.s.l. Total annual precipitation is about 3400 mm (medium value 1998–2007, data from ETESA, 8.10.2008) with a dry season approximately from December to April of the following year, as well as a rainy season from May to November.

The vegetation in the area of the trail originally was a semideciduous tropical lowland forest with elements of a gallery forest, about 300 m away from the river Majagua. The area was deforested more than 100 years ago and is now used mainly for rearing cattle. In addition to trampling by cattle and people, the habitat is affected by cutting, occasional passing cars, the application of herbicides, and fire during the dry season. The vegetation is mostly herbaceous with some trees at the borders of the trail. On one side, the trail borders a secondary forest (about 100 years old) for about 200 m (Fig. 1b). The collecting activity was performed by walking along the trail and searching for plants or fungi on and close to the trail within a distance of about 2–3 m on either side, up to a maximum height of ca. 2 m. Therefore, epiphytic plants were only marginally registered.

For the inventory of plants, vascular plants (seed plants and ferns, not mosses) were considered. For the inventory of fungi, all fungi in a broad sense were searched for, including Myxomycetes (slime moulds) and Peronosporomycetes (downy mildews), evident in the field by macroscopic fruiting bodies or by structures visible with a hand lens. Samples of dead leaves, rotten fruits, and decaying fruits were taken to the lab for scrutiny under a stereomicroscope.

The following ecological groups of fungi and niches were investigated:

- saprotrophic fungi on dead plant material, like dead wood (trunks, branches, twigs), litter, flowers, and fruits on and above the soil, as well as on excrements, termite nests, and dead animals (mainly insects);
- parasitic or commensal fungi on living plant organs, like leaves, flowers, fruits, bark, branches, and roots as far as accessible;
- fungi parasitic on animals;
- fungi living on other fungi (fungicolous);
- mutualistic fungi, like mycorrhizal and lichenized fungi. The latter, however, are underrepresented because no lichenologist participated during fieldwork.

All taxa were collected at least once for identification and the elaboration of herbarium specimens. Well known taxa were later recorded by a mark in a list of records and photos were taken for comparison. The technical processing of the plant specimens of one sampling event took about 1 day, while the morphological documentation of the collections of fungi took about 3–5 working days after each sampling event. Specimens of plants were identified mainly with the help of the Flora of Panama (Woodson et al. 1943–1980) and other literature (e.g. Hammel 2003; Morales 2003), by comparison with plant specimens housed in the National Herbarium of Panama (PMA), and with the help of specialists (R. Mangelsdorff, R. Rincón, M. Stapf, and further members of staff of PMA). Fungi were identified based on numerous different publications (e.g. Guzmán and Piepenbring 2011 and citations therein), and with the help of specialists. G. Kost focused on the identification of species of agaricoid *Basidiomycota*, T.A. Hofmann on the identification of species of *Asterinaceae* and other plant parasitic species of Dothideomycetes, T.A. Hofmann and M. Piepenbring on species of *Meliolales* and *Pucciniales* in collaboration with O. Perdomo, E. Yilmaz, and R. Mangelsdorff. R. Lücking and H. Sipmann provided some names for lichens and R. Kirschner for fungi belonging to different systematic groups. The lists of more or less preliminarily identified species of plants and fungi are provided in the Appendices 1 and 2 respectively. For authors of scientific names of plants see Correa et al. (2004), for

those of scientific names of fungi see Index Fungorum (www.indexfungorum.org). Specimens of plants are deposited in the Herbarium of the Universidad Autónoma de Chiriquí (U.CH.), duplicates of species new for the Chiriquí province additionally in the National Herbarium of Panama (PMA). Specimens of fungi will be deposited at the National Herbarium (PMA) as well as the Botanische Staatssammlung, Munich, Germany (M) as soon as their identification is ascertained.

Knowledge on the geographical distribution of plant species in Panama is documented by Correa et al. (2004). The plant species list (Appendix 1) is compared to these data and records new to Panama or Chiriquí province are identified.

The first checklist of fungal species known for Panama was published by Piepenbring (2006) and recently made accessible as an updated online resource by Piepenbring (2011). This database is used to identify new records of fungal species for Panama among the reliably identified species listed in Appendix 2.

One record corresponds to the observation of one species during one sampling event (2 h), so the possible maximum number of records of a given species in the present context is 24. The number of records of a given species is used as a measure of relative abundance of this species rather than its absolute abundance. When a sexual and an asexual form are known to belong to the same fungal species, this species is called by its sexual name. If functional diversity and ecology of fungi is analyzed, however, sexual and asexual forms should be considered separately, because they often occupy distinct ecological niches. For *Xylariales*, asexual forms were not considered, because they most probably belong to sexual forms considered in the list, but could not be assigned to them with certainty in the context of the present investigation.

Smoothed (randomised or rarefied) species accumulation curves (SAC) were calculated with the 'vegan' package (Oksanen et al. 2010) of the R environment (R Development Core Team 2010) to display the accumulation of species when the number of records increases (Gotelli and Colwell 2001). By the analysis of the curves' shape (e.g. initial slope, approaching an asymptote or not), it is possible to evaluate basic patterns of species richness as well as sampling efforts. The number of species observed is displayed for each sampling event and trend lines are calculated for these data. The species richness estimators Chao1, Jackknife1, and Bootstrap (e.g. reviewed in Colwell and Coddington 1994) were calculated in R, too. By analysing the estimator curves' shape, an extrapolated species richness is considered a serious estimation only if its value remains stable, i.e. if the respective curve shows a stable asymptote for a considerable part at the right end of the analysis. All data used here (Appendices 1, 2) as well as the R source code (Appendix 3) and the R data for species of plants (Appendix 4) and fungi (Appendix 5) are provided as electronic supplementary material.

Results

In the context of the present investigation in secondary tropical vegetation in western Panama, 311 species of vascular plants were detected by approximately 4,000 records, which correspond to one new species every 13th record (Appendix 1). Approximately 567 species of fungi were distinguished based on 1,614 records, corresponding to one new species every third record (Appendix 2). Except *Dioscorea spiculiflora* and *Paspalum botterii*, all plant species are already known for Panama (Correa et al. 2004), 54 species and infraspecific taxa are cited for the first time for the Chiriquí province in western Panama. Among the fungal species, 17 species and one variety are cited for the first time

for Panama, at least two species probably represent species new to science. New species and further new records of fungi will be published in a taxonomic context.

Patterns of species accumulation for plants and fungi during sampling events differ fundamentally as shown by the species accumulation curves (Fig. 2) and in the non-logarithmized rank-abundance plot (Fig. 3). The species accumulation curve for plants reaches an asymptote, so the list of vascular plant species for the site is close to complete. The number of fungi continues to rise steeply with each sampling event (Fig. 1a). Non-saturating species accumulation curves were also observed when fungi on dead wood, living leaves, bark, leaf litter, and soil were analyzed separately (figures not shown).

The numbers of recorded species per sampling event (grey curves in Fig. 1b, c) follow similar patterns for plants and fungi with two peaks (ca. 10th and 20th sampling), mainly due the influence of climate (rainy vs. dry season). These numbers result in a steadily rising trend line, which means that there is a tendency of more species recorded during the next than during the previous sampling event, corresponding to a "learning effect" and an increasing efficiency of recording.

Rank abundance plots (Fig. 3) reveal an unequal distribution of abundant and rare fungi with 285 (50%) singletons and 101 (18%) duplicates, whereas the records of plant species are equally distributed among the sampling events (Fig. 3). The large number of rarely recorded species of fungi, visible as "right tail" is typical for hyperdiverse and/or undersampled communities.

Species richness estimators predicted 310–318 plant species (Fig. 4a) and provided values in the range of the observed species richness. Species richness estimations for fungi varied strongly depending on the estimator function (686–1,013 species; Fig. 4b). None of the estimator curves approached saturation.

The recorded 311 species of plants belong to at least 77 different families, with the *Fabaceae* (32 species, 10% of total species of plants), *Poaceae* (20 species, 6%), and *Asteraceae* (19 species, 6%) being the most important ones with respect to species richness. *Acrocomia aculeata*, *Anacardium excelsum*, *Bursera simaruba*, *Cordia alliodora*, *Gliricidia sepium*, and *Ocotea veraguensis* are examples of trees typical for the area. *Centrosema pubescens*, *Chromolaena ivifolia*, *Davilla kunthii*, and *Serjania mexicana* represent the relatively abundant lianas and *Anthurium cubense*, *Dimerandra emarginata*, as well as *Tillandsia fasciculata* are typical epiphytes. Apart from several species of

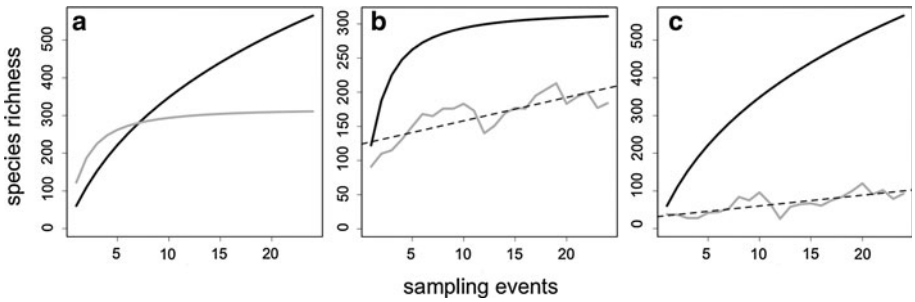

Fig. 2 Rarefied species accumulations curves for vascular plants and fungi recorded during 24 sampling events in western Panama. **a** Direct comparison of species richness of fungi (*black*) and plants (*grey*). **b** Plants and **c** fungi: Rarefied accumulation curves (*black*) and numbers of species recorded per sampling event. The *dashed grey lines* correspond to *regression lines* showing the statistical increase in species recognition per sampling event

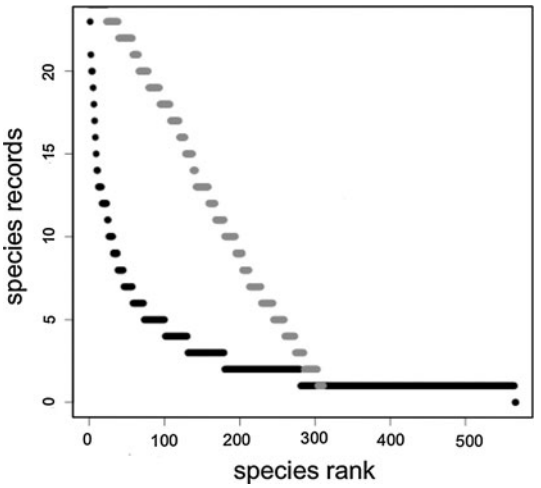

Fig. 3 Rank-abundance plot (*Whittaker plot*) for fungi (*black*) and plants (*grey*) recorded during 24 sampling events in western Panama

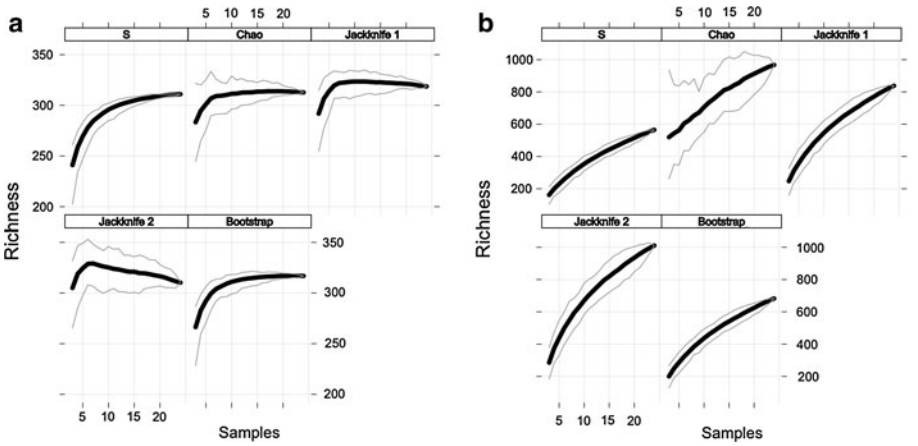

Fig. 4 Estimator curves for plants (**a**) and fungi (**b**) recorded during 24 sampling events in western Panama. S is the accumulation curve of observed species richness

Cyperaceae and *Poaceae*, the herbs *Desmodium incanum* and *Elephantopus mollis* are present with numerous individuals, among many other species.

Most species of 567 species of fungi recorded in the context of the present investigation belong to the *Ascomycota* (192 species, 34%), the *Basidiomycota* (209 species, 37%), and asexual forms (147 species, 26%). Within the *Ascomycota*, the *Meliolales* (34 species, 6% of the total number of species; Fig. 1d), the *Xylariales* (29 species, 5%; Fig. 1c), *Phyllachorales* (18 species, 3%), and *Hypocreales* (17 species, 3%) are represented with relatively high species richness. Within the *Basidiomycota*, the most important groups are the *Agaricales* (99 species, 17%; Fig. 1f), *Polyporales* (37 species, 7%; Fig. 1g), and with respect to plant parasitic microfungi the *Pucciniales* (23 species, 4%). In total, there are about 303 (53%) species of microfungi, of which about 172 species (30%) are probably plant parasitic microfungi, including the group of cercosporoid fungi (asexual forms of *Mycosphaerellaceae*, *Capnodiales*; Fig. 1e) which is highly diverse with 32 species (6%).

Most plant parasitic species of microfungi are specific for a single host species on the site, nine species were found on two species of host plants. This information, however, is preliminary, because many specimens have not been conclusively identified.

Numerous interactions among fungi and of fungi with other organisms were observed. One particularly impressive example is shown in Fig. 1h. On a gall caused by the rust fungus *Pucciniosira dorata*, five organisms interact within a space of a few millimeters, i.e. the rust and its host plant (*Triumfetta* cf. *lappula*), two fungicolous, asexual fungi (*Acremonium* sp., *Tuberculina* sp.), and a larva of *Cecidomyiidae* (*Insecta*) feeding on the fungi.

Discussion

In the context of the present study, we recorded 311 species of vascular plants and 567 species of fungi corresponding to a ratio of 1:1.8. This value, however, is preliminary and will definitely increase with additional sampling effort, since the species accumulation curve for fungi as well as its estimator curves did not saturate at all. A precise total fungal species richness of the area cannot be inferred from the available data. This conclusion for fungal diversity is similar to results of other efforts directed towards fungal inventories and confirms the fact that fungi correspond to a hyperdiverse group of organisms (e.g. Pirozynski 1972; Schmit and Lodge 2005). Assuming a ratio of up to six fungal species per plant species (Hawksworth 1991, 2001) would mean in this instance that up to 1,866 fungal species can be expected, many of them not accessible to direct observation, such as endophytic or soil microfungi.

Pegler (1997), a mycologist with broad experience on tropical macrofungi, states that it is unlikely that more than one in ten species of macrofungi can be recognized by name in a tropical rain forest. Therefore, the task of inventorying a tropical area is enormous and only few mycologists accept the challenge. To make one example, Chaverri and Vílchez (2006) were only able to identify 44 of 87 species of *Hypocreales* (*Ascomycota*) in a Costa Rican study despite their expertise in this group. It is therefore not surprising that many of our specimens still lack definite identifications, with only 152 species (27%) recorded in the context of the project so far having a more or less reliable scientific name.

For all fungal taxa inventories we need more taxonomic expertise, more monographs with keys for identification, and collaboration among mycologists (e.g. Hawksworth and Mueller 2005). By detailed monographic investigation including the revision of type specimens, numerous further specimens, literature, and molecular data, species concepts can change and thereby change the results of the analysis of species richness. Narrow concepts lead to higher and broad concepts to lower estimations of species diversity.

The recorded number of fungal species of *Basidiomycota* is nearly equal to that of *Ascomycota*, despite that about twice as many species of *Ascomycota* are known to science (Kirk et al. 2001). Reasons for this situation are that species of *Basidiomycota* develop more conspicuous fruiting bodies so they were more easily collected during fieldwork and that the systematic position of the asexual forms of fungi was not determined. The dominance of species of *Meliolales*, *Phyllachorales*, and *Pucciniales* among plant parasitic microfungi is typical for neotropical habitats, as shown by Piepenbring et al. (2011). More than 50% of the species recorded for our Majagua site are microfungi, but in an all taxa inventory, they might correspond to more than 80% (Schmit and Mueller 2007). Their relative number will certainly increase, when more sophisticated methods of isolation, especially culturing and bait methods (Rossman et al. 1998; Mueller et al. 2004), are used to increase the knowledge of species.

The present study should be carried on by continuous sampling, including culturing and bait methods, as well as by improving the taxonomic identifications by study of literature, herbarium specimens, and by collaboration with specialists. Names are indispensable to integrate the data of the present study into the body of mycological knowledge, which includes aspects of morphology, ecology, distribution, and phylogeny. The data will allow an analysis of seasonal changes and of the patterns of variation of fungal fructification—aspects important to estimate the diversity of fungi (Lodge and Cantrell 1995a, b).

The question which was the starting point for the present investigation apparently is simple: How many species of plants and fungi are present in the selected area? In order to obtain the answer, however, many years of arduous work and the involvement of numerous specialists with a broad knowledge of species and ecology of plants and fungi are necessary. All people repeatedly involved in the present investigation not only learnt to recognize numerous species of plants and fungi, their phenology and ecology, but also became aware of the incompleteness of our knowledge, developing a deep respect for nature. Diversity assessments, like the present case study, are important for capacity building, conservation strategies, and decision making to preserve fungi by the protection of unique habitats (Rossman 1997).

Acknowledgments The authors thank numerous students and colleagues who collaborated in the field, namely J. M. Andrade, K. Araúz, G. Bethancourt, E. Caballero, L. Cáceres, O. Cáceres, V. Carrión, S. Castillo, D. Cruz, M. Cuevas, J. Espinosa, A. Gockele, A. K. Gómez, J. González, L. González, B. Henríquez, R. Kirschner, M. Mastrolinardo, L. Mayorga, E. Miranda, N. Moran, J. de Quiel, J. Ramos, I. de Rincón, S. Rudolph, L. Saldaña, K. Samaniego, I. Samudio, G. Steinbeisser, and J. Weisenborn. For identification of plants we are grateful to R. Mangelsdorff, R. Rincón, M. Stapf, and further members of the staff of the herbarium PMA, for the identification of fungi we were supported by K. Araúz, J. Fournier, R. Kirschner, R. Lücking, O. Perdomo, H. Sipmann, T. Trampe, N. Völxen, and E. Yilmaz. We thank R. Mangelsdoff for interesting discussions and help to improve the manuscript. S. Cronje improved the English of the manuscript. The institutional support of the Universidad Autónoma de Chiriquí (UNACHI), the National Authority of the Environment (ANAM, Panama), and the German Academic Exchange Service (DAAD) is acknowledged.

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