

4 The Potential Role of Above-Ground Biodiversity Indicators in Assessing Best-Bet Alternatives to Slash and Burn

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Improvements in agricultural productivity usually are counterproductive to maintaining or enhancing indigenous biodiversity. Habitat loss, the main factor associated with biodiversity decline, increases with intensive, permanent, large-area cropping systems. Biodiversity continues to be reduced globally, partly because it is consistently undervalued and partly because of the lack of sufficient incentives for its retention and maintenance (UNEP/CBD 2002). Major contributing factors are the extraordinarily high biotic complexity in tropical forested lands and difficulties in devising and implementing cost-efficient methods for biodiversity survey and evaluation. Few published data demonstrate significant links between biodiversity and ecosystem dynamics in a way that can be used to attach a meaningful value to biodiversity or to provide related landscape-based indicators of profitability.

Against this background Alternatives to Slash and Burn (ASB) has sought readily observable field indicators that can be used to assess the status of nutrient dynamics and help forecast the impact of a specified land use on biodiversity and net primary productivity. To be acceptable to management, methods of biodiversity assessment must be cost-effective and easy to implement. Although a truly generic means of rapid biodiversity assessment remains elusive, surveys using newly developed protocols along comparable, putative land use intensity gradients in different global ecoregions have generated improved baseline datasets that provide new insights into response couplings between biodiversity and land use condition (Gillison and Liswanti 1999; Gillison 2000a). This is a significant point of entry into exploring the next important step: the biodiversity–profitability dynamic. Apart from local and regional needs, a global challenge for developing generic assessment methods is to facilitate the comparison of vegetation response to environmental change between different continents where environment and plant adaptation may be similar but where species differ. In this way

lessons learned in one region may be translated to another, thereby improving the information feedback loop to farmers and enhancing international dialogue on alternatives to slash-and-burn. For management and planning to be effective, assessment techniques should be readily transferable and should deliver interpretable results with tangible, practical outcomes.

The ASB ecoregional studies to date conclude that managers and planners should be better empowered to assess their existing resources to improve management practices. This strategy should provide a more acceptable, rational, and scientific basis for adapting management to meet unpredicted changes in the physical environment caused by events such as El Niño extremes, war, change in governments, or price shocks in global and regional markets. This chapter discusses the need to improve the efficiency of existing vegetation survey and classification methods and the ways in which these methods can be integrated with multitaxon surveys to identify, calibrate, and test appropriate biodiversity indicators. Finally, case studies from tropical, lowland rainforest environments illustrate ways in which policymakers and managers can use the outcomes from these procedures in selecting more attractive alternatives to slash-and-burn.

The need to conserve biodiversity is reflected in the mission of the international Convention on Biological Diversity (CBD), which highlights a demand for improved methods of assessing biodiversity and an understanding of the nexus between biodiversity and socioeconomic incentives (UNEP/CBD 2002). Despite the clear need to develop a science-based, practical framework for biodiversity conservation, there is as yet no operational definition for biodiversity. As Weitzman (1995:21) points out, the implementation of any plan to preserve biodiversity is hampered by the lack of an operational framework: "We need a more-or-less consistent and useable measure of the value of biodiversity that can tell us how to trade off one form of diversity against another." Miller and Lanou (1995) maintain that the issue of attaching a value to biodiversity is governed largely by the interaction between human society and biodiversity. This implies that there should be a demonstrable, dynamic link between biodiversity and productivity for human needs (UNEP/CBD 2002). And although the World Bank (1995) has made a case for integrating biodiversity concerns into national decision making, the mechanisms for achieving this remain elusive. In Indonesia, as in many other developing countries, the government recognizes that a lack of scientific and management expertise is a serious impediment to biodiversity conservation (Government of Indonesia 1993). This constraint is further aggravated by the current policies of property rights on public lands and waters and the failure to use much of the financial returns from the use of the country's natural living resources (e.g., via logging) to support biodiversity conservation (Barber et al. 1995; see also chapter 13, this volume). These concerns highlight the need not only for a working definition of biodiversity but also for a cost-efficient, generic, science-based tool for its assessment. Both should aim to provide practical outcomes for government and corporate policy planners and managers involved in natural resource management.

BIODIVERSITY INDICATORS

THE NEED

One of the tenets of rapid biodiversity assessment (RBA) is that for practical purposes there should be readily observable indicators or surrogates of more complex plant and animal assemblages. Whether this is a pious hope or a genuine possibility is a continuing source of debate (Cranston and Hillman 1992; Reid et al. 1993; Pearson 1995; Howard et al. 1996; Lawton et al. 1998). For example, there may be questionable theoretical support for targeting so-called keystone or flagship species (Tanner et al. 1994; Williams 2002). It can be argued that without a clear understanding of multi-dimensional, causal relationships or trophic webs, simple, linear correlations between singular, ecosystem variables such as woody plant basal area and primates may lead to incorrect forecasts of land use impact. On the other hand, comparative estimates of ecosystem variables such as soil nutrients, soil structure, plant species richness, and richness of plant and animal functional types can provide important insights into ecosystem behavior and biodiversity when examined along key environmental gradients (Gillison 1981; Gillison and Brewer 1985; Wessels et al. 1998).

An in-depth study of biodiversity conservation in Ugandan forests led Howard et al. (1996, 1997) to conclude that although the value of indicators and their ability to provide an accurate assessment of biodiversity within a particular site remain debatable, practical factors compel their use. Thus much importance is placed on selecting appropriate indicator groups for which selection criteria involve ease of sampling and availability of resources (Howard et al. 1996, 1997). In similar vein, Miller et al. (1995) argue for reduced, manageable attribute sets that can be used to convey more complex information such as the status of key pollinators and seed dispersers that may not be available at the time of survey. In the absence of experimental data, an inescapable outcome is that demonstrating indicator efficiency entails, at the very least, calibration from intensive baseline studies of taxa and functional types at a comprehensive range of spatial, temporal, and environmental scales. But because traditional survey methods attract high logistic costs, such studies are almost nonexistent in complex tropical environments. And depending on environmental context and the variables used, surveys may demonstrate conflicting, correlative trends between biotic and abiotic variables. For example, a multitaxon baseline study of Sumatran rainforests (Gillison et al. 1996), showed that whereas plant biodiversity increased with elevation from 500 to 900 m above sea level, the converse was true for insects and birds. Although such confounding effects can be accommodated in part by appropriate regression models and site stratification, predictive models of biodiversity based on environmental correlates such as elevation must be evaluated carefully before being adopted by managers. It follows that environmental context and scale are critical in designing field studies of biodiversity and interpreting the results (see also He et al. 1994). This

chapter briefly discusses the relative merits of certain forms of biodiversity indicators in a specific environmental context. These include Linnean species, functional types, diversity indexes, and measurable elements of vegetation structure.

SPECIES

Despite recent advances in the use of alternative indicators, the species remains the most widely used currency for biodiversity assessment. Other species-based approaches may use higher taxa such as families or genera (Prance 1995) or a measure of phylogenetic distance that includes taxic richness or genealogical relationships embodied in taxonomic classifications, typically by weighting the relative number of species per genus, genera per family, and so on (Vane-Wright et al. 1991; Williams et al. 1992; Faith 1995). In complex, tropical lowland forests, however, species identification can be difficult, costly, and time-consuming. For this and other ecological reasons there is growing concern that as long as the species remains the preferred indicator, there will be little progress in biodiversity assessment (cf. Wulff 1943; Heywood and Baste 1995). When used in isolation from other, more dynamic descriptors of organism behavior and performance, species richness and abundance can seriously misinform and distort biodiversity assessment. Parity in richness alone between sites does not guarantee equivalence in either genetic composition or genetically determined, adaptive response to environment. Yet from a conservation management perspective, response characterization of individuals to environmental impact should form an important benchmark for assessing biodiversity and the degree to which biodiversity is affected by external factors such as disturbance and habitat modification. Therefore there is a clear need for other biotic descriptors that offer a reasonable alternative or complement to the use of species in biodiversity assessment.

FUNCTIONAL TYPES

Partly through increasing dissatisfaction with species as sole indicators, an emerging school of thought now holds that biodiversity or other forms of ecological assessment should include functional aspects of individuals as well as species (Box 1981; Gillison 1981, 1988; Nix and Gillison 1985; Cowling et al. 1994a, 1994b; Huston 1994; Collins and Benning 1996; Martinez 1996; Woodward et al. 1996). Diaz (1998:18) regards functional types (FTs) as “sets of organisms showing similar responses to environmental conditions and having similar effects on the dominant ecosystem processes” (see also Cramer et al. 1999). This is an extension of an earlier definition by Shugart (1997:20), who used plant functional types (PFTs) “to connote species or groups of species that have similar responses to a suite of environmental conditions.” Varying definitions of FTs are most commonly associated with guilds (organisms that share the same resources) (Gillison 1981; Bahr 1982; Huston 1994; Gillison and Carpenter

1997; Gitay and Noble 1997; Mooney 1997; Shugart 1997; Smith 1997; Smith et al. 1997). But as Martinez (1996:115–116) asserts, “The functional aspects of biodiversity are a broad and vague concept that needs substantial added specification in order to become scientifically more useful.” According to Cramer (1997), the task of screening all the world’s species for FTs is impossible, and for a global model, a breakdown of the world’s vegetation can be achieved only based on major physiognomic or otherwise recognizable features. Such views are rapidly changing; Cramer et al. (1999) now argue that PFTs may be considered a necessary and appropriate simplification of species diversity, with the added advantage that ecosystem types often correspond naturally with PFT assemblages.

Gillison (1981) devised a method of assembling plant functional attributes (PFAs) into a functional modus or PFT and demonstrated correlations between PFTs or modi and landscape disturbance patterns. A formal, generic approach for characterizing vascular plants as PFTs from combinations of a basic set of thirty-five PFAs was developed by Gillison and Carpenter (1997:Appendix). Whereas species identification, especially in complex tropical forests, demands botanical expertise that is often unavailable, PFTs can be applied by observers with limited botanical and ecological experience.

PLANT FUNCTIONAL TYPES

As described by Gillison and Carpenter (1997), PFTs or functional modi are combinations of essentially adaptive morphologic or functional attributes (e.g., leaf size class, leaf inclination class, leaf form and type [distribution of chlorophyll tissue]) coupled with a modified Raunkiaerean life form and the type of above-ground rooting system. The PFTs are derived according to a specific grammar or rule set from a minimum set of thirty-five functional attributes. An individual with microphyll-sized, vertically inclined, dorsiventral leaves supported by a phanerophyte life form would be a PFT expressed as MI-VE-DO-PH. Although they tend to be indicative for a species, they are independent of species in that more than one species can occur in one PFT and more than one PFT in a species. The PFTs allow the recording of genetically determined, adaptive responses of plant individuals that can reveal intraspecific as well as interspecific response to environment (e.g., land use) in a way that is not usually contained in a species name. Because they are generic, they have a singular advantage in that they can be used to record and compare datasets derived from geographically remote regions where, for example, adaptive responses and environments may be similar but where species differ.

Functional characteristics can be used to compare adaptive properties between individuals and sets of individuals independently of species, for example, where taxa may be geographically disjunct but where individuals possess similar adaptations to environment. In a comparative study of methods of characterizing site productivity and growth patterns in North Queensland rainforests (Vanclay et al. 1996), the PFT-based approach was more efficient in estimating site productivity potential for

commercial tree species than traditional methods of site characterization based on species and vegetation structure. Consistently high correlations have been demonstrated between total numbers of species and total numbers of unique PFT plots across a wide range of environments (Gillison et al. 1996; see also Baskin 1994). The implications from these studies are that for surveys where taxonomic expertise is lacking, PFTs can be used to predict species richness with a high degree of confidence should this be needed. This may also benefit rapid assessment of plant biodiversity and improve correlations between plant and animal biodiversity (cf. Gillison et al. 1996). A field technique (the VegClass procedure, Gillison 2001, 2002) embodying this approach and designed specifically for rapid survey is now available for use by observers with minimal training. This technique enables rapid characterization of site physical features, vegetation structure, species composition, and PFTs and is supported by a training manual and a software package that facilitates data compilation and analysis (Gillison 2002).

DIVERSITY MEASURES AND INDEXES

Plant species richness (the number of species per unit area) can be a useful descriptor of animal habitat but does not in itself reflect evenness or dominance of species, as do the frequently used diversity indexes of Shannon-Wiener and Simpson (Magurran 1988). Despite the widespread application of these complex indexes, ecologists rarely agree about their interpretive value. For this reason, species richness is still the most commonly applied diversity index in biodiversity studies, although the search for more ecologically meaningful indexes continues (Cousins 1991; Majer and Beeston 1996). Most diversity indexes are based on species abundance (number of individuals per species) and at best are usually regarded as a species-based stand attribute with potentially low ecological information. Generating such indexes entails time-consuming counts of individuals, which is rarely cost-effective, especially in rapid surveys of complex, tropical forested landscapes. To circumvent this problem, Gillison et al. (1999; see also Gillison 2000a) developed a method for calculating Shannon-Wiener, Simpson's, and Fisher's alpha diversity indexes based primarily on PFT data. Unlike several other approaches (e.g., Martinez 1996), this has the advantage that in rapid survey it is the number of species per PFT rather than numbers of individuals (abundance) per species that is counted in each plot. Using PFTs alone, a measure of plant functional complexity (PFC) developed by the same authors can be computed as a functional numeric distance between PFT assemblages derived from a table of weighted transformation values between specific PFAS (Gillison and Carpenter 1997; Gillison 2000a). The PFC value can be used to discriminate between two plots where species and PFT richness are similar but where PFT composition varies. Such discrimination is potentially useful in discriminating between successional sequences in forest types or between widely differing vegetation types such as mediterranean heaths and tropical forests with similar PFT and species richness. Under such circumstances measures such as PFC can add useful information to biodiversity assessment.

VEGETATION STRUCTURE

Vegetation classification and survey methods typically combine broad structural variables with seasonality (e.g., evergreenness, deciduousness) and a list of dominant species or higher taxa, as in “Very tall evergreen Dipterocarp forest.” Although this may be relevant for geographic purposes, it is inappropriate for management at a 1:50,000 mapping scale. In addition, structurally similar interregional vegetation types rarely contain the same plant species. Although vegetation structure may be used to predict animal habitat within a region, sites with similar vegetation structure in widely separated ecoregions are not necessarily ecologically equivalent. Where enhanced sensitivity is needed to discriminate between biodiversity patterns within and between regions, additional attributes such as PFTs can provide the necessary value-added discriminants.

THE LANDSCAPE AS A SAMPLING FRAMEWORK FOR BIODIVERSITY INDICATORS

Given that plant and animal taxa and FTs tend to be distributed throughout a variety of land use mosaics, the landscape matrix seems to be a logical framework for studying biodiversity (cf. Forman and Godron 1986; Franklin 1993). This is the underlying concept for survey design and data collection across all the ASB ecoregional benchmark sites. Because landscape disturbance is a critical determinant of biodiversity (Petraitis et al. 1989; van der Maarel 1993; Phillips et al., 1994), factors such as agriculture, shifting cultivation, and forest fragmentation should be considered in survey design (Grime 1979; Bierregard et al. 1992; Sayer and Wegge 1992; Margules and Gaston 1994; Brooker and Margules 1996; Margules and Pressey 2000). For this reason ASB ecoregional sites are located as far as possible along representative, successional gradients of land use and vegetation types, from pristine rainforest and logged-over forest to plantations and degraded grasslands. These successional or so-called land use intensity transects have been generally called chronosequences in ASB (chapter 2, this volume).

Within landscapes, the issue of plot size selection continues to be argued among plant ecologists. Although plot size may vary typically from 1 to 50 ha (Dallmeier 1992; Condit 1995), some studies show that for characterizing plant diversity, useful information can be recorded from complex, humid tropical forest plots as small as 50 by 2 m (Parker and Bailey 1991; Parker and Carr 1992; Parker et al. 1993) or 40 by 5 m (Gillison et al. 1996). At landscape mosaic scale, efficiency in biodiversity survey usually is improved through the application of many small plots rather than a few large plots (cf. Keel et al. 1992). Whereas large (e.g., 50-ha plots) tend to focus only on tree species and mask important fine-scale habitat variability, a 40- by 5-m plot, or multiples of them, can be used to record all vascular plant species and positioned to target organisms with restricted or specific environmental ranges (e.g., streambanks, ridge crests, and forest margins). Environmental variability at this typically complex

scale demands cost-effective survey techniques (cf. Margules and Haila 1996) where cost efficiency is governed by the nature of the variables being recorded as well as management scale and purpose. In selecting best-bet options for sustainably managing biodiversity and productivity, a manager or planner needs access to a variety of management procedures with forecastable outcomes across a variety of landscape facets. For this reason, the largely stochastic nature of landscape biodiversity dynamics requires that samples should include the widest possible environmental range of taxa and functional types. This may include a variety of land use types (LUTs) ranging from largely unaltered to highly modified forests, home gardens, and intensive agricultural plots to degraded grasslands. Within a region or subregion other factors such as climate (temperature, light, moisture), drainage, and soil gradients also play a significant role in survey design.

METHODS

FIELD STUDIES

Ecoregional land use intensity gradients were investigated in Brazil, Cameroon, and Indonesia. These contained LUTs, also called meta-land use systems in ASB, and lowland, forested landscape mosaics that are common in many tropical developing countries. The study was implemented at two levels: The first compared broad-scale, plant-based biodiversity patterns across similar LUTs in the three ecoregions using a standardized survey protocol. At a second and much more detailed level, the Indonesian ecoregion was subjected to an intensive biophysical, multitaxon (plant and animal) biodiversity baseline study. Sites in the three benchmark areas included sixteen in Jambi Province, Central Sumatra, mainly on ultisols but ranging across intact and logged-over rainforests, rubber plantations, jungle rubber, softwood timber plantations, agricultural subsistence gardens, and farmed *Imperata* grassland (cassava and other crops) to degraded *Imperata* grassland (table 4.1). In Brazil, twenty-five sites were located along a similarly putative but more widely distributed land use intensity gradient mainly in the western Amazon Basin (Rondônia–Acre). These ranged from logged-over rainforest on acid soils of moderate to poor fertility (ultisols) through coffee (*Coffea canephora* Pierre ex. Fröhner L.), cacao (*Theobroma cacao* L.), and rubber plantations in various combinations with other agricultural and agroforestry crops, to newly established subsistence gardens. To include a more comprehensive gradient of soil features, other sites were added to include short-stature, closed forests (campinharana) on leached sands (spodosols) north of Manaus and shrubby heaths on lithosolic sandstone soils (psamments), an oil palm plantation on a latosol (oxisol), and a semi-closed woodland savanna (cerradão) on an oxisol near Brasília (table 4.2). In Cameroon in humid tropical West Africa, twenty-one sites were located primarily along a regional, rainfall seasonality gradient from rainforest in the south at Awae, Akok, and Mbalmayo, extending north through Yaoundé to include sub-Saharan savanna

Table 4.1 Site Physical Environment and Vegetation Features in Jambi Province, Indonesia

Site Number	Location	Latitude (DMS)	Longitude (DMS)	Elevation (m)	Land Use Type	Mean Canopy Height (m)	Crown Cover (%)	Mean Basal Area, All Woody Plants (m ² /ha)	PFTs	Plant Species	Species per PFT
BS01	Pasir Mayang	01-04-47 S	102-06-02 E	76	Intact rainforest (outside BIOTROP permanent plot)	21	75	27.33	35	102	2.91
BS02	Pasir Mayang	01-04-45 S	102-05-53 E	60	Intact rainforest (BIOTROP permanent plot)	20	65	32.67	35	101	2.89
BS03	Pasir Mayang	01-04-43 S	102-05-55 E	85	Logged over 1984 (old log ramp secondary forest)	10	35	13.33	24	50	2.08
BS04	Pasir Mayang	01-04-53 S	102-06-09 E	60	Logged over 1979–1980 (secondary forest)	24	80	32.67	39	108	2.77
BS05	Pasir Mayang	01-04-56 S	102-06-05 E	75	Logged over 1983 (secondary forest)	28	70	27.33	38	111	2.92
BS06	Pasir Mayang	01-04-59 S	102-06-43 E	65	<i>Panseriambes falcataria</i> plantation 1993–1994	6	40	6.00	28	43	1.54
BS07	Pasir Mayang	01-03-09 S	102-08-10 E	55	<i>Panseriambes falcataria</i>	16	30	8.00	33	46	1.39

Table 4.1 (Continued)

Site Number	Location	Latitude (DMS)	Longitude (DMS)	Elevation (m)	Land Use Type	Mean Canopy Height (m)	Crown Cover (%)	Mean Basal Area, All Woody Plants (m ² /ha)	PFTs	Plant Species	Species per PFT
BS08	Pasir Mayang	01-05-25 S	102-07-05 E	53	Rubber monoculture	11	65	14.67	37	66	1.78
BS09	Pasir Mayang	01-05-27 S	102-06-56 E	53	Rubber monoculture plantation (8 yr)	12	70	15.33	30	54	1.80
BS10	Pancuran Gading	01-10-12 S	102-06-50 E	30	Jungle rubber (15–38 yr)	14	50	18.00	47	112	2.38
BS11	Pancuran Gading	01-10-13 S	102-06-46 E	30	Jungle rubber (15–38 yr)	14	50	20.67	41	97	2.37
BS12	Kuamang Kuning	01-35-58 S	102-21-11 E	40	Tall <i>Imperata</i> grassland	1	90	0.01	10	11	1.10
BS13	Kuamang Kuning	01-35-56 S	102-21-12 E	40	Short <i>Imperata</i> grassland	1	90	0.01	5	7	1.40
BS14	Kuamang Kuning	01-36-05 S	102-21-22 E	48	Cassava plantation	1.8	50	0.10	12	15	1.25
BS15	Kuamang Kuning	01-36-00 S	102-21-21 E	48	Cassava plantation	1.8	40	0.10	13	19	1.46
BS16	Pancuran Gading	01-10-13 S	102-06-58 E	30	<i>Chromolaena, Clibadium</i> 4-yr fallow	2	95	0.10	32	43	1.34

DMS, degrees, minutes, and seconds; PFT, plant functional type; BS, Bina Samaktha plots now referred to as SUM (Sumatra) sites; BIOTROP, Southeast Asian Regional Centre for Tropical Biology.

Table 4.2 Site Physical Environment and Vegetation Features in Brazil

Site Number	Location	Latitude (DMS)	Longitude (DMS)	Elevation (m)	Land Use Type	Mean Canopy Height (m)	Crown Cover (%)	Mean Basal Area, All Woody Plants (m ² /ha)	PFTs	Plant Species	Species per PFT
BRA01	Ji Parana, Rondônia	10-55-23 S	61-57-25 W	230	Agroforestry plot, rubber and coffee, 12 yr old	8	45	8.67	13	16	1.23
BRA02	Ji Parana, Rondônia	10-55-23 S	61-57-25 W	230	Agroforestry plot, rubber and coffee, 12 yr old	8	45	8.00	13	15	1.15
BRA03	Ji Parana, Rondônia	10-55-14 S	61-58-27 W	225	<i>Brachyaria</i> pasture, natural forest cleared 20 yr ago	0.8	95	0.03	10	12	1.20
BRA04	Ji Parana, Rondônia	10-55-14 S	61-58-27 W	225	<i>Brachyaria</i> pasture, natural forest cleared 20 yr ago	0.8	95	0.03	9	14	1.56
BRA05	Ji Parana, Rondônia	10-58-30 S	62-00-58 W	265	<i>Schizolobium</i> (bandarra) & <i>Coffea robusta</i> plantation	22	30	7.33	19	27	1.42
BRA06	Ji Parana, Rondônia	10-58-30 S	62-00-58 W	265	<i>Schizolobium</i> (bandarra) and <i>Coffea robusta</i> plantation	21	40	7.33	19	27	1.42

Table 4.2 (Continued)

Site Number	Location	Latitude (DMS)	Longitude (DMS)	Elevation (m)	Land Use Type	Mean Canopy Height (m)	Crown Cover (%)	Mean Basal Area, All Woody Plants (m ² /ha)	PFTs	Plant Species	Species per PFT
BRA07	Theobroma, Rondônia	10-06-18 S	62-11-40 W	230	Capoéira–cassava plantation (after slash-and-burn)	2.2	15	0.50	29	34	1.17
BRA08	Theobroma, Rondônia	10-06-12 S	62-11-40 W	230	<i>Inga edulis</i> plantation	5	90	8.67	21	32	1.52
BRA09	Theobroma, Rondônia	10-06-12 S	62-11-40 W	230	Capoéira– <i>Cassia siamea</i> plantation	4.5	95	7.00	17	21	1.24
BRA10	Theobroma, Rondônia	10-06-40 S	62-11-58 W	242	Rubber and coffee plantation with mixed fruit trees	8	15	5.00	15	17	1.13
BRA11	Theobroma, Rondônia	10-06-40 S	62-11-58 W	240	Rubber and coffee plantation with mixed fruit trees	8	10	3.33	15	16	1.07
BRA12	Theobroma, Rondônia	10-13-03 S	62-23-49 W	252	Secondary rainforest	22	85	18.00	39	79	2.03
BRA13	Reca, Rondônia	09-46-48 S	66-37-44 W	287	Mixed agroforestry plantation: cupuaçu, <i>Bactris</i> , and Brazil nut	12	40	13.33	33	50	1.52
BRA14	Reca, Rondônia	09-46-48 S	66-37-44 W	287	Mixed agroforestry plantation: cupuaçu, <i>Bactris</i> , and Brazil nut	12	40	11.33	33	47	1.42
BRA15	Reca, Rondônia	09-46-48 S	66-37-43 W	232	New subsistence garden, slash-and-burn, <i>Bactris</i>	0.4	10	0.01	20	26	1.30
BRA16	Reca, Rondônia	09-46-48 S	66-37-43 W	232	New subsistence garden, slash-and-burn, <i>Bactris</i>	0.4	10	1.00	20	23	1.15
BRA17	Pedro Peixoto, Acre	10-01-13 S	67-09-39 W	270	Moderately disturbed rainforest, grazed	26	90	22.33	44	80	1.82

BRA18	Pedro Peixoto, Acre	10-01-13 S	67-09-39 W	295	Secondary forest: capoëira (3–4 yr after maize garden)	12	95	16.00	32	63	1.97
BRA19	Pedro Peixoto, Acre	10-01-13 S	67-09-39 W	295	Secondary forest: capoëira (3–4 yr after maize garden)	12	95	11.67	43	82	1.91
BRA20	Pedro Peixoto, Acre	10-01-03 S	67-09-27 W	316	>10-yr-old <i>Brachiaria</i> <i>brizantha</i> pasture	0.2	95	0.01	12	18	1.50
BRA21	Pedro Peixoto, Acre	10-01-03 S	67-09-27 W	316	>10-yr-old <i>Brachiaria</i> <i>brizantha</i> pasture	0.2	95	0.10	10	14	1.40
BRA22	Jardin do Botanica	—	—	100	Low, semievergreen vine thicket, woodland, some bromeliads	4.50	70	13.33	36	90	2.50
BRA23	Presidente Figueiredo Igarape do Iajés	01-59-39 S	60-01-34 W	130	Shrubby heath, moderately disturbed	2.50	80	2.67	28	36	1.29
BRA24	Reserva Biológica de Campina	02-35-21 S	60-01-55 W	120	Campinharana (intact forest on white sand)	0	80	18.67	25	44	1.76
BRA25	Embrapa Acre	02-53-34 S	59-58-21 W	120	15- to 18-yr oil palm (<i>Elaeis guineensis</i>) plantation	7.50	35	20.00	21	24	1.14

DMS, degrees, minutes, and seconds; PFT, plant functional type; BRA, Brazil.

Table 4.3 Site Physical Environment and Vegetation Features in Cameroon

Site no.	Location	Latitude (DMS)	Longitude (DMS)	Elevation (m)	Land Use Type	Mean Canopy Height (m)	Crown Cover (%)	Mean Basal Area, All Woody Plants (m ² /ha)	PFTs	Plant Species	Species per PFT
CAM01	Awae Village	03-36-05 N	11-36-15 E	657	Secondary forest, heavily disturbed	20.00	70	18.00	43	103	2.40
CAM02	Awae	03-36-05 N	11-36-15 E	657	2-yr <i>Chromolaena</i> fallow	2.50	95	2.00	37	61	1.65
CAM03	Awae	03-36-05 N	11-36-15 E	657	New garden with groundnut and cassava	0.40	5	0.50	19	20	1.05
CAM04	Awae	03-36-05 N	11-36-15 E	657	8- to 10-yr <i>Chromolaena</i> fallow	3.50	95	4.67	35	54	1.54
CAM05	Nkol-fulu	03-55-31 N	11-35-49 E	696	Secondary forest, heavily disturbed	12.00	95	7.33	33	50	1.52
CAM06	Nkol-fulu Mefou and Afamba Department	03-55-31 N	11-35-49 E	696	4-yr <i>Chromolaena</i> fallow	2.60	95	2.17	22	30	1.36
CAM07	Nkol-fulu Mefou and Afamba Department	03-55-41 N	11-35-49 E	696	New cultivation, egusi melon	0.40	30	4.67	12	14	1.17
CAM08	Mengomo (Ebolowa Station)	02-34-45 N	07-02-05 E	554	Secondary forest, heavily disturbed	18.00	70	20.67	42	93	2.21

CAM09	Mengomo (Ebolowa Station)	02-34-37 N	11-01-29 E	576	2-yr <i>Chromolaena</i> fallow	2.50	95	0.50	47	76	1.62
CAM10	Mengomo (Ebolowa Station)	02-34-37 N	11-01-29 E	576	>45-yr-old jungle <i>Cacao</i>	12.00	75	17.33	47	80	1.70
CAM11	Akok (Ebolowa Station)	02-42-19 N	11-16-09 E	554	2-yr <i>Chromolaena</i> fallow	2.30	95	1.50	50	71	1.42
CAM12	Akok	02-42-27 N	11-16-30 E	554	1-yr garden	2.00	90	1.00	55	78	1.42
CAM13	Akok (Ebolowa Station)	02-43-08 N	11-17-05 E	585	4-yr <i>Chromolaena</i> fallow	3.50	95	1.00	66	100	1.52
CAM14	Akok	02-43-12 N	11-16-58 E	585	2-yr <i>Chromolaena</i> fallow	2.50	95	1.00	44	61	1.39
CAM15	Akok (Ebolowa Station)	02-42-45 N	11-16-42 E	559	>30-yr <i>Cacao</i> plantation	18.00	75	20.00	43	63	1.47
CAM16	Bafia (20 km after Bafia)	04-48-58 N	11-10-27 E	560	1-yr cassava field	2.50	50	2.00	37	51	1.38
CAM17	Makam III–Batoum II	05-02-40 N	10-42-04 E	977	Humid savanna	3.00	70	2.00	41	47	1.15
CAM18	Nkometou II	04-04-51 N	11-33-17 E	596	1-yr <i>Chromolaena</i> fallow	1.80	98	0.20	29	45	1.55
CAM19	Near Bafia	04-48-56 N	11-10-25 E	640	Shrub savanna	4.00	8	0.67	18	25	1.39
CAM20	Nkolitam	03-28-21 N	11-29-25 E	600	<i>Raffia</i> palm swamp	18.00	90	14.00	29	57	1.97
CAM21	Akok “Enuzam”	02-42-45 N	11-16-45 E	550	Old secondary forest	20.00	85	26.00	41	57	1.39

DMS, degrees, minutes, and seconds; PFT, plant functional type; CAM, Cameroon.

sites (Makham III), with the soils in the southern zone being primarily ultisols. Along this gradient LUTs ranged from closed, logged, and community-managed rainforest, through cacao plantations and agricultural subsistence gardens with varying fallow systems, to cassava and maize in farmed savanna, to nonagricultural woodland savanna (table 4.3).

Within each ecoregional gradient, sites were located according to the gradient-based or gradient-oriented transect (gradsect) method of Gillison and Brewer (1985). With gradsects, sites are located according to a hierarchical nesting of presumed key physical environmental determinants such as climate, elevation, parent rock type, soil, vegetation type, and land use. Because the distribution of plants and animals is determined mainly by environmental gradients, the gradsect approach offers a means of sampling such variation. In most cases where the intent is to maximize information about environmental variability and species distribution in the area, the method is logistically much more efficient than surveys based on purely random or purely systematic grid designs (Gillison and Brewer, 1985) and is finding increasing application in regional surveys (Austin and Heyligers 1989, 1991; Sorrells and Glenn 1991; Green and Gunarwadana 1993; USGS 2001; FAO 2002). In addition, the sampling of environmental gradients rather than discrete, non-gradient-oriented samples tends to enhance efficiency of extrapolative spatial models by ensuring a more comprehensive coverage of environmental range. Although the method was originally designed and evaluated for vegetation survey, more recent, comparative assessments indicate that the gradsect approach also performs more efficiently for fauna than many other survey procedures (Wessels et al. 1998).

At each location, a standardized vegetation survey method (modified from Gillison 1988 and updated in part by Gillison and Carpenter 1997; Gillison 2002) was used to record a minimum set of biophysical characteristics (table 4.4) and determine the species and PFT for each plant (see appendix). In each case, the data were recorded along a 40- by 5-m strip transect located along the prevailing topographic contour. In the Sumatran site an intensive, multitaxon baseline study was undertaken across all land use types by a group of animal and plant specialists. Above- and below-ground biodiversity was assessed (large and small mammals, birds, insects, soil macrofauna, and vascular plants) in addition to soil physicochemical variables and above-ground carbon. The vegetation transect was the focal point for all other specialist studies (details of methods are available in Gillison 2000a).

DATA ANALYSIS

Data were compiled using a laptop computer and a recently developed software package, VegClass (Gillison 2001), that facilitates compilation of PFTs according to the rule set of Gillison and Carpenter (1997). The Windows-based software provides a means of recording all field data according to a standardized format. These include all site physical and vegetational features listed in table 4.4. In addition, the VegClass

Table 4.4 List of Data Variables Recorded for Each 40- by 5-m Plot

Site Feature	Descriptor	Data Type
Location reference	Location	Alphanumeric
	Date (dd-mm-yr)	Alphanumeric
	Plot number (unique)	Alphanumeric
	Country	Text
Observer(s)	Observer(s) by name	Text
Physical	Latitude (deg.min.sec., GPS)	Alphanumeric
	Longitude (deg.min.sec., GPS)	Alphanumeric
	Elevation (m a.s.l., aneroid and GPS)	Numeric
	Aspect (compass degrees, perpendicular to plot)	Numeric
	Slope percentage (perpendicular to plot)	Numeric
	Soil depth (cm)	Numeric
	Soil type (U.S. soil taxonomy)	Text
	Parent rock type	Text
	Litter depth (cm)	Numeric
	Terrain position	Text
Site history	General description and land use or landscape context	Text
Vegetation structure	Vegetation type	Text
	Mean canopy height (m)	Numeric
	Crown cover percentage (total)	Numeric
	Crown cover percentage (woody)	Numeric
	Crown cover percentage (nonwoody)	Numeric
	Cover abundance (Domin) of bryophytes	Numeric
	Cover abundance of woody plants <1.5 m tall	Numeric
	Basal area (mean of 3, m ² /ha)	Numeric
	Furcation index (mean and coefficient of variation % of 20)	Numeric
Profile sketch of 40- by 5-m plot (scannable)	Digital image	
Plant taxa	Family	Text ^a
	Genus	Text ^a
	Species	Text ^a
	Botanical authority	Text ^a
	If exotic (binary, presence–absence) ^b	Numeric
PFT	Plant functional elements combined according to published rule set	Text ^a
Quadrat listing	Unique taxa and PFTs per quadrat (for each of 8 [5- by 5-m] quadrats) ^b	Numeric
Photograph	Hard copy and digital image ^b	Digital and hard copy image

GPS, global positioning system; PFT, plant functional type.

^aSummary of presence–absence by site for numerical analyses.

^bNot available for all sites.

software facilitates on-demand data summaries and graphs of desired combinations of variables within and between plots that can be exported to industry-standard spreadsheet and relational database software. For data recorded for each contiguous 5- by 5-m quadrat within the 40- by 5-m transect, graphs of cumulative species and PFT totals per unit area can be generated to allow the subjective inspection of asymptotic curves as an indicator of sample efficiency for a specific vegetation type or LUT (Gillison 2002). If needed, the sampling procedure can be used to discriminate between successional stages of vegetation independently of species. And because it contains adaptive morphological (PFT) as well as taxonomic attributes, VegClass exhibits a higher sensitivity to changes in environment than more traditional classification methods. The same software was used to calculate PFT-based, Shannon-Wiener, Simpson's, and Fisher's alpha indexes as well as PFC.

The most efficient vegetation correlates of animal distribution acquired from an intensive multitaxon survey in Central Sumatra were obtained by linear regression (Pearson product moment) between all attribute values using the Minitab (version 13.32) software package. The most efficient plant-based predictors of animal taxa overall were plant species richness, PFT richness, species richness:PFT richness ratio, mean canopy height, and basal area of all woody plants. Using a method of multidimensional scaling (MDS) of these variables (Belbin 1992) based on a Gower metric similarity measure, the two best eigenvector solutions were extracted for each ecoregional dataset. These vectors were then plotted as a two-dimensional display of relative site distribution. With this procedure, the raw data variables can be back-correlated against each vector axis to determine their relative contribution to overall pattern should this be needed. The data from all ecoregional sites were then pooled and the MDS procedure repeated to display the relative distribution for the entire dataset.

As an additional exploratory measure, for each ecoregional dataset, the same MDS procedure was used to extract the best single eigenvector. The single eigenvalues thus acquired were standardized and ranked on a 1–10 scale for each site in order to identify any biodiversity-related trend according to an intuitive ranking of land use intensity gradients. For Brazil this was restricted to twenty-one sites in the Rondônia–Acre region of the western Amazon Basin to focus on a more constrained pattern of land use. These ranked values were used as an integrated vegetation index (V-index) (Gillison 2000a). The V-index is used here as an additional, potentially useful predictor for biodiversity; high values indicate more complex vegetation structure and richness in species and PFTs. For this reason V-index values were included in the correlative analyses of the Sumatran multitaxon baseline study.

RESULTS AND DISCUSSION

In the Sumatran sites, richness in both plant species and PFTs, mean canopy height, basal area, and cover abundance of understory woody plants were the most efficient predictors of fauna (table 4.5). Among the better indicators there is a clear tendency

Table 4.5 Linear Correlations^a Between Richness of Plant Species, PFTs and Their Ratios, and Various Animal Taxa and Above-Ground Plant Carbon

Faunal Groups	Plant Species	PFT	Species per PFT	PFC	V-Index	Shannon	Simpson	F-Alpha	Mean Canopy Height (m)	Basal Area (m ² /ha)	Crown Cover (%)	WPIts	FI
Ground-Dwelling Arthropods													
Termite abundance	0.844	0.732	0.944	0.654	0.810	0.687	-0.643	-0.656	0.832	0.872	0.384	0.748	-0.767
	0.017	0.061	0.001	0.111	0.096	0.088	0.119	0.109	0.080	0.054	0.524	0.053	0.130
Termite species	0.849	0.705	0.976	0.564	0.811	0.650	-0.630	0.564	0.900	0.869	0.481	0.773	-0.813
	0.016	0.077	0.000	0.187	0.096	0.114	0.122	0.187	0.038	0.056	0.412	0.041	0.094
Canopy Arthropods													
Acari	0.190	-0.232	0.443	-0.465	0.328	-0.662	0.624	-0.648	0.356	0.427	0.154	0.622	-0.704
	0.576	0.493	0.172	0.150	0.325	0.027	0.040	0.031	0.283	0.190	0.651	0.041	0.016
Blattodea	0.124	-0.014	0.204	-0.061	0.086	-0.452	0.563	-0.456	-0.010	0.075	-0.287	0.554	-0.060
	0.716	0.966	0.548	0.858	0.801	0.162	0.071	0.158	0.977	0.827	0.392	0.077	0.861
Coleoptera	0.312	0.458	0.127	0.481	0.166	0.075	0.231	-0.093	0.016	0.111	-0.026	0.453	0.416
	0.350	0.156	0.709	0.134	0.625	0.826	0.494	0.785	0.963	0.746	0.940	0.162	0.203
Collembola	0.643	0.089	0.882	-0.130	0.776	-0.374	0.402	-0.720	0.799	0.768	0.567	0.729	-0.739
	0.033	0.795	0.000	0.703	0.005	0.258	0.221	0.013	0.003	0.006	0.069	0.011	0.009
Diptera	0.038	0.404	-0.197	0.350	-0.035	0.279	0.002	0.261	-0.066	0.077	0.179	-0.158	0.453
	0.912	0.217	0.562	0.291	0.918	0.406	0.995	0.438	0.847	0.821	0.597	0.644	0.161
Formicidae	0.274	0.370	0.142	0.426	0.121	0.082	0.145	-0.054	-0.040	0.030	-0.235	0.576	0.234
	0.415	0.262	0.676	0.191	0.723	0.810	0.671	0.875	0.906	0.929	0.487	0.064	0.489
Formicidae, total	0.371	0.572	-0.052	0.829	0.069	0.713	-0.724	-0.045	-0.177	-0.158	-0.391	0.005	0.522
	0.538	0.313	0.933	0.021	0.912	0.072	0.066	0.924	0.776	0.799	0.524	0.993	0.366
Hemiptera	0.098	0.229	-0.026	0.254	0.005	0.073	-0.032	0.161	-0.039	-0.061	-0.495	0.507	-0.245
	0.774	0.499	0.920	0.454	0.988	0.832	0.925	0.637	0.910	0.858	0.121	0.111	0.469
Hymenoptera	0.302	0.446	0.129	0.426	0.169	0.068	0.194	-0.063	0.061	-0.075	-0.105	0.560	0.207
	0.367	0.169	0.705	0.192	0.619	0.843	0.567	0.854	0.858	0.827	0.759	0.074	0.541

Table 4.5 (Continued)

Faunal Groups	Plant Species	PFT	Species per PFT	PFC	V-Index	Shannon	Simpson	F-Alpha	Mean Canopy Height (m)	Basal Area (m ² /ha)	Crown Cover (%)	WPIts	FI
Canopy Arthropods													
Isoptera (canopy)	0.417	0.140	0.496	0.192	0.519	-0.134	0.132	-0.308	0.652	0.444	0.289	0.076	-0.409
	0.203	0.681	0.121	0.571	0.102	0.695	0.698	0.337	0.030	0.171	0.389	0.824	0.212
Neuroptera	-0.038	-0.267	0.172	-0.323	0.161	-0.509	0.527	-0.443	0.279	0.271	0.464	-0.313	-0.212
	0.911	0.428	0.613	0.333	0.636	0.110	0.096	0.172	0.406	0.419	0.151	0.349	0.532
Orthoptera	0.545	0.378	0.528	0.395	0.467	-0.223	0.432	-0.531	0.380	0.345	-0.025	0.709	-0.154
	0.083	0.252	0.095	0.229	0.147	0.509	0.185	0.093	0.249	0.298	0.942	0.014	0.651
Psocoptera	0.398	0.148	0.457	0.019	0.451	-0.457	0.019	-0.562	0.458	0.471	0.353	0.535	-0.019
	0.225	0.664	0.157	0.956	0.164	0.158	0.956	0.072	0.157	0.144	0.287	0.090	0.956
Spiders	0.186	0.307	0.050	0.298	0.097	-0.066	0.307	-0.042	0.011	0.074	-0.162	0.484	0.184
	0.584	0.359	0.884	0.374	0.776	0.847	0.358	0.903	0.973	0.829	0.635	0.131	0.588
Thysanoptera	0.470	0.756	0.138	0.693	0.244	0.426	-0.099	0.061	0.066	0.124	0.020	0.416	0.352
	0.144	0.007	0.685	0.018	0.470	0.191	0.772	0.859	0.847	0.717	0.954	0.203	0.289
Insects, total	0.593	0.487	0.526	0.529	0.515	0.002	0.261	-0.287	0.395	0.422	0.078	0.667	-0.036
	0.055	0.129	0.096	0.094	0.105	0.995	0.438	0.392	0.229	0.196	0.819	0.025	0.916
Insects, unidentified	0.771	0.418	0.839	0.439	0.820	-0.101	0.294	-0.483	0.773	0.774	0.429	0.545	-0.406
	0.005	0.201	0.001	0.177	0.002	0.768	0.380	0.133	0.005	0.005	0.188	0.083	0.216
Bird spp., total	0.599	0.347	0.704	0.306	0.661	0.157	-0.157	-0.370	0.726	0.625	0.291	0.442	-0.244
	0.040	0.269	0.011	0.334	0.019	0.627	0.627	0.237	0.008	0.024	0.447	0.150	0.445
Above-ground carbon ^b	0.796	0.558	0.909	0.484	0.771	0.383	-0.295	-0.380	0.792	0.730	0.626	0.382	-0.535
	0.000	0.025	0.000	0.057	0.005	0.143	0.268	0.147	0.004	0.011	0.039	0.145	0.090

PFT, plant functional type; PFC, plant functional complexity; V-index, vegetation index; Shannon, Shannon-Wiener diversity index for PFTs; Simpson, Simpson's diversity index for PFTs; F-Alpha, Fisher's alpha diversity index for PFTs; WPIts, cover abundance of woody plants <1.5 m tall; FI, mean furcation index canopy trees.

^aCorrelation r value on first line of each cell. Probability value on second line.

^bAbove-ground carbon data from Hairiah and van Noordwijk (2000).

for the species:PFT ratio rather than species or PFT richness alone to improve prediction for above-ground carbon and for certain animal groups such as birds, collembolans, and termites. There is no clear ecological reason as to why this ratio should be a better predictor. However, one can speculate that higher ratios in the later and more complex successional stages of forest development reflect less available above-ground ecological niche space for larger (more readily measurable) organisms where more species are represented by fewer PFTs.

When the general pattern of plant and animal taxonomic distribution along the LUTS is examined, it is evident that the highest biodiversity richness occurs in certain pristine forest types and in the more disturbed jungle rubber. This may be explained partly by the nature of the available ecological niches in both. The jungle rubber plots have both higher species and PFT richness than the older growth forests but a lower species:PFT ratio. Whereas the former has allowed the development of cryptic terrestrial and arboreal habitats over a longer time frame, the younger and more dynamic jungle rubber displays a much wider variety of ecological niches and canopy gap openings where the fragmentary nature of the stand is maintained mainly by frequent disturbance from humans and to a much lesser extent by large mammals such as elephants and tapirs. This is consistent with the intermediate disturbance hypothesis, which states that highest species richness will occur in zones of intermediate disturbance rather than in old growth.

Although the high correlations for many variables do not in themselves provide a valid argument for identifying cause and effect, in this study the traditional hypothesis that richness begets richness is consistent with forest successional trends and the coevolution of increasingly complex food webs and abundance of autotrophs and heterotrophs including detritivores. The distribution of plant cellulose, as represented by mean canopy height, basal area, and above-ground carbon, along a land use intensity gradient corresponds closely with species and abundance of ground-dwelling termites, and this may be explained in part by termite feeding habits (see also Bignell et al. 2000; Jones et al. 2002).

In surveys of tropical forested landscapes, meaningful correlates between plants and birds can be difficult to achieve (Jepson and Djarwadi 2000; Beehler et al. 2001), and in temperate regions investigations using plant functional groups to predict bird distribution can be inconclusive (cf. Abernethy et al. 1996). This study may be the first of its kind to reveal the potential of a newer suite of plant-based variables to predict bird species richness across a range of LUTS in tropical, forested landscapes. Table 4.5 reveals highly significant correlations between bird species richness, plant species richness, species:PFT richness ratio, mean canopy height, basal area, and V-index. When bird species richness is correlated with the ratio of mean canopy height to furcation index (FI) of canopy woody plants (indicative of branching density) the correlation r value increases to 0.792 ($p = .006$), indicating that bird species richness may be a function of both canopy height and “branchiness.” A regression of bird species richness against combined mean canopy height and FI gave a significant R^2 of 53.2

Table 4.6 Plant-Based Linear Correlates^a with Soil Physicochemical Attributes^b

	pH-H ₂ O	pH-KCl	Organic C (%)	N _{tot} , %	K	Na	Mg	Al	EC/EC	Al _{sat}	Bulk Density
Mean canopy height	-0.719	-0.828	0.486	0.386	0.005	-0.205	-0.370	0.632	0.441	0.558	-0.770
	0.002	0.000	0.056	0.140	0.984	0.446	0.159	0.009	0.087	0.025	0.000
Basal area (m ² /ha)	-0.684	-0.780	0.503	0.395	0.048	-0.198	-0.347	0.684	0.491	0.595	-0.784
	0.004	0.000	0.047	0.130	0.859	0.462	0.188	0.003	0.053	0.015	0.000
Crown cover (%)	0.215	0.125	0.092	0.095	-0.063	0.076	0.278	-0.057	-0.107	-0.089	-0.120
	0.424	0.644	0.737	0.728	0.818	0.779	0.298	0.833	0.694	0.743	0.659
WPlts	-0.285	-0.206	0.502	0.376	0.475	0.381	0.300	0.296	0.512	0.137	-0.627
	0.284	0.445	0.048	0.151	0.063	0.146	0.259	0.265	0.043	0.614	0.009
Cover abundance of bryophytes	-0.593	-0.777	0.459	0.526	0.097	-0.164	-0.300	0.697	0.584	0.527	-0.743
	0.016	0.000	0.074	0.037	0.720	0.545	0.260	0.003	0.018	0.036	0.001
FI	0.172	0.293	-0.144	-0.026	0.093	0.175	0.180	-0.123	-0.094	-0.074	0.291
	0.525	0.270	0.594	0.925	0.732	0.516	0.504	0.651	0.728	0.786	0.274
PFT	-0.402	-0.471	0.878	0.742	0.609	0.393	0.097	0.643	0.880	0.279	-0.890
	0.123	0.066	0.000	0.001	0.012	0.132	0.720	0.007	0.000	0.295	0.000

Total plant species	-0.550	-0.653	0.716	0.550	0.329	0.104	-0.225	0.687	0.650	0.484	-0.868
Species per PFT	0.027	0.006	0.002	0.027	0.214	0.700	0.403	0.003	0.006	0.058	0.000
V-index	-0.683	-0.745	0.405	0.278	-0.012	-0.196	-0.463	0.616	0.353	0.602	-0.742
PFC	0.004	0.001	0.120	0.298	0.966	0.466	0.071	0.011	0.180	0.014	0.001
Shannon	0.664	0.755	-0.611	-0.477	-0.174	0.056	0.291	-0.688	-0.575	-0.544	0.852
Simpson	0.005	0.001	0.012	0.061	0.520	0.838	0.274	0.003	0.020	0.029	0.000
F-alpha	-0.283	-0.387	0.855	0.722	0.714	0.503	0.084	0.589	0.865	0.208	-0.843
	0.288	0.162	0.000	0.002	0.002	0.047	0.757	0.016	0.000	0.444	0.000
	0.352	0.231	-0.507	-0.496	-0.545	-0.327	-0.348	-0.366	-0.732	-0.049	0.615
	0.181	0.390	0.045	0.051	0.029	0.217	0.186	0.163	0.001	0.858	0.011
	-0.367	-0.309	0.722	0.661	0.647	0.445	0.327	0.479	0.866	0.100	-0.767
	0.162	0.244	0.002	0.005	0.007	0.084	0.216	0.060	0.000	0.712	0.001
	0.488	0.542	0.240	0.174	0.585	0.633	0.876	-0.348	0.290	-0.651	-0.018
	0.055	0.030	0.370	0.519	0.017	0.009	0.000	0.187	0.276	0.006	0.946

N_rot, total nitrogen; ECEC, effective cation exchange capacity; Al_sat, aluminum saturation; WP1ts, cover abundance of woody plants <1.5 m tall; Bryo, cover abundance of bryophytes; FI, mean furcation index of canopy trees; PFT, plant functional types; V-index, vegetation index; PFC, plant functional complexity; Shannon, Shannon-Wiener diversity index for PFTs; Simpson, Simpson's diversity index for PFTs; F-alpha, Fisher's alpha diversity index for PFTs.

^aLinear correlation r value on first line of each cell, probability value on second line.

^bSoil analytical data from Hairiah and van Noordwijk (2000).

percent. This potential has been demonstrated in a similar, independent ASB study in northern Thailand (Gillison and Liswanti 1999).

Table 4.6 outlines correlations between plant-based variables and a range of soil physicochemical variables; only the most statistically significant are listed. These include highly significant correlations between certain soil variables such as bulk density, pH, organic carbon, total nitrogen and aluminum, species and PFT richness, vegetation structure, and V-index. There is no immediate explanation as to why these soil attributes correspond more closely than others with both plant species and PFT richness. Land use practices also confound speculation about the biodiversity–soil nutrient dynamic. In Jambi, Sumatra, for example, total soil nitrogen is highest in monoculture rubber plantations (added artificial fertilizer), with only moderate species and PFT richness, and in the (unfertilized) jungle rubber plots (plots 10 and 11, table 4.1) that are richest in plant taxa and PFTs. Among the soil variables, bulk density corresponds most closely with species and PFT richness. Although diversity indexes are rarely accepted without question as biodiversity indicators, in the present study each of the PFT-based, Shannon-Wiener, Simpson's, and Fisher's alpha values is significantly correlated with a variety of key soil variables (table 4.6). The reasons underlying this correlative pattern warrant study if cause-and-effect relationships are to be better understood.

Evidence of plant morphological adaptation such as PFAs (and by association PFTs) to varying soil nutrient conditions is widely documented along gradients of salinity, pH, total and available nitrogen, phosphorus, and potassium and in certain extreme soil and parent rock mineral complexes such as limestone and serpentinites. These are characterized among well-documented plant assemblages such as “calicolous” or “serpentinite” flora. Despite clear trends between PFTs and the nutrient and physical substrate, physiological explanations for these phenomena usually are extraordinarily complex (Larcher 1975) and are likely to be further confounded by soil–climate interaction. Apart from the correlates revealed here for humid, lowland tropical forested lands, in boreal forests pH and soil organic matter content are considered to be among the best soil-related predictors of biodiversity (Koptsik et al. 2001). Nevertheless, the Sumatran study suggests that, for this area at least, despite a lack of evidence for cause and effect, the utility of plants as indicators of biodiversity and related soil nutrient availability (and hence potential agricultural productivity) is clearly enhanced by the use of species richness, PFT richness, and their ratios both individually and in combination. When combined with vegetation structural predictors of animal distribution (such as mean canopy height and basal area) these plant-based attributes become potentially powerful indicators of animal habitat. Whereas terrestrial animal diversity is governed largely by plants, in the study area, plant-based diversity in turn can be shown to vary predictably with soil nutrients as well as pH and bulk density across all LUTs. The Sumatran study does not aim to provide generic soil-based indicators of biodiversity or to elucidate soil–plant dynamics. But it has produced a readily testable hypothesis that certain soil variables are distributed in a predictable way with certain

key plant and animal assemblages. If this model can be shown to hold, it will have positive implications for adaptive management.

Multidimensional scaling of sites in Indonesia, Cameroon, and Brazil using the plant-based variables listed in tables 4.1, 4.2, and 4.3 (with the exception of crown cover percentage) reveal tight clustering of complex agroforests adjacent to intact forest. In Indonesia these are represented by jungle rubber (figure 4.1), in Cameroon by both jungle and mixed *Cacao* plantations (figure 4.2), and in Brazil by complex agroforests containing cupuaçú, coffee, *Bactris* palm, and Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.) (figure 4.3). These clusters represent best-bet agroforestry scenarios in each country. The ordinations (figures 4.1, 4.2, and 4.3) that compare similar LUTS in Brazil, Cameroon, and Indonesia reveal consistent trends between plant-based biodiversity in complex agroforests and jungle rubber and *Cacao* along land use intensity gradients. These are clearly evident when examined in the context of gradient extremes between degraded or highly simplified grasslands (including improved pastures) and intact forest. When the datasets from each ecoregion are combined and the MDS repeated (figure 4.4), a central zone for best bets is indicated, with the separation between agroforests reflected mainly by regional differences in species richness and with Sumatra and Cameroon indicating higher forest species and PFT richness than the Brazilian sites sampled in this study.

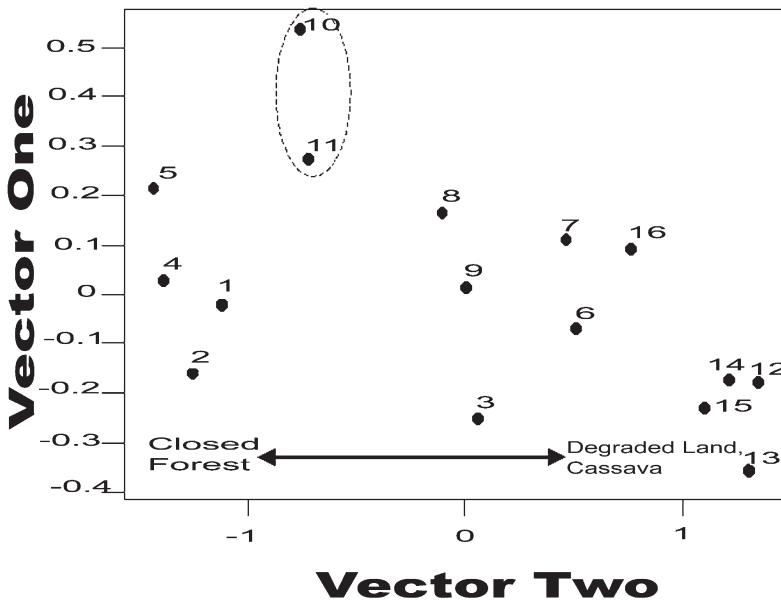


Figure 4.1 Multidimensional scaling of 16 plots along a land use intensity gradient in Sumatra. Dashed lines indicate area of best-bet alternatives to slash-and-burn (in this case jungle rubber). See table 4.1 for plot details and context of land use types.

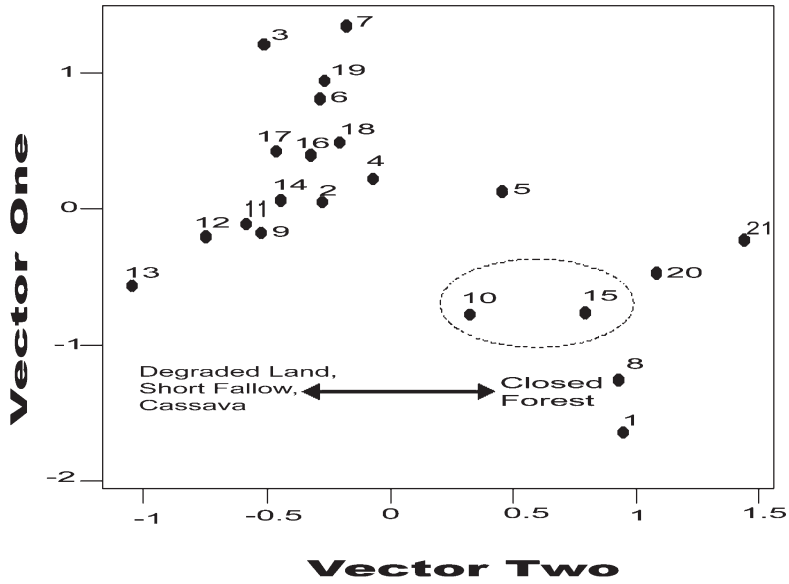


Figure 4.2 Multidimensional scaling of 21 plots along a land use intensity gradient in Cameroon. Dashed lines indicate area of best-bet alternatives to slash-and-burn (in this case periodically tended *Cacao* plantation and jungle *Cacao*). See table 4.3 for plot details and land use types.

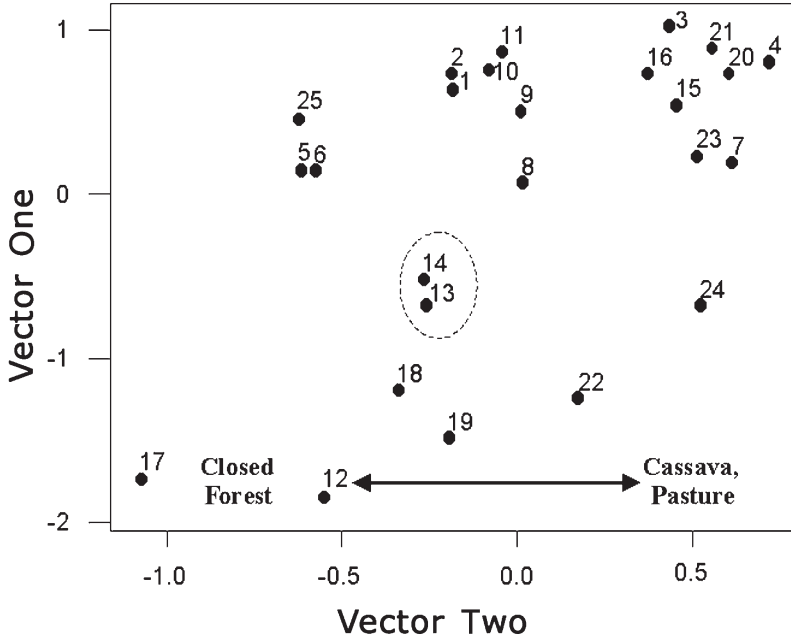


Figure 4.3 Multidimensional scaling of 25 plots along land use intensity gradient in Brazil. Dashed lines indicate area of best-bet alternatives to slash-and-burn (in this case periodically tended, mixed agroforestry plantation: cupuaçu, *Bactris*, and Brazil nut). See table 4.2 for plot details and context of land use types.

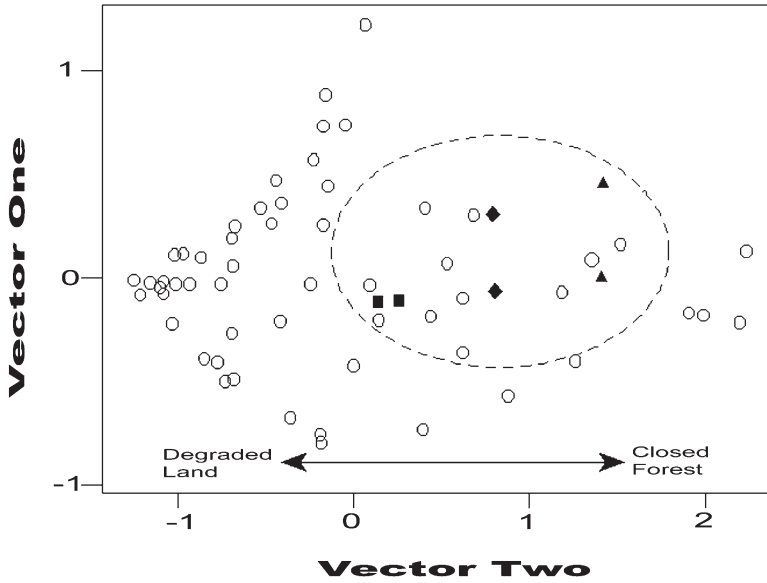


Figure 4.4 Multidimensional scaling of site data from all three ecoregions showing relative positioning of relative best-bet agroforests in Sumatra (solid triangles), Cameroon (solid diamonds), and Brazil (solid squares).

The V-index values for each ecoregion (figures 4.5, 4.6, and 4.7) reflect patterns of vegetation complexity that correspond with an intuitive assessment of land use intensity and, in the case of Sumatra, with patterns of plant and animal biodiversity. As expected, across all ecoregions, similar values for low-productivity land use such as cassava (*Manihot exculenta* Crantz) and degraded grassland are evident at the lowest index values, with highest values recorded for older-growth and secondary forests. The V-indexes are not designed to produce generic values for LUTs but rather a relative within-region index that may be potentially useful in regional planning. It is of interest nonetheless that the two most similar land use gradients (Sumatra and Cameroon) present similar V-index values for best-bet jungle rubber (Jambi sites 10 and 11, with V-indexes of 7.9 and 7.6, respectively) and jungle cacao and 30-year-old plantation cacao (Cameroon sites 10 and 15, with V-indexes of 7.0 and 7.7, respectively). The Brazilian mixed agroforest plots 13 and 14 have V-indexes of 6.4 and 6.0, respectively with higher values of 7.8 occurring in Capoeira secondary forest (forest that has reinvaded abandoned pasture land). The lower values for the Brazilian agroforests may reflect age since establishment (7–8 years) where V-indexes can be expected to increase with time but also the more intensively managed nature of the Brazilian systems. Although the V-index is an integrated measure of vegetation complexity (species, PFTs, and structure) rather than biodiversity, the high correlations between V-indexes and animal groups, especially birds (table 4.5), suggests it may have a useful role in biodiversity assessment.

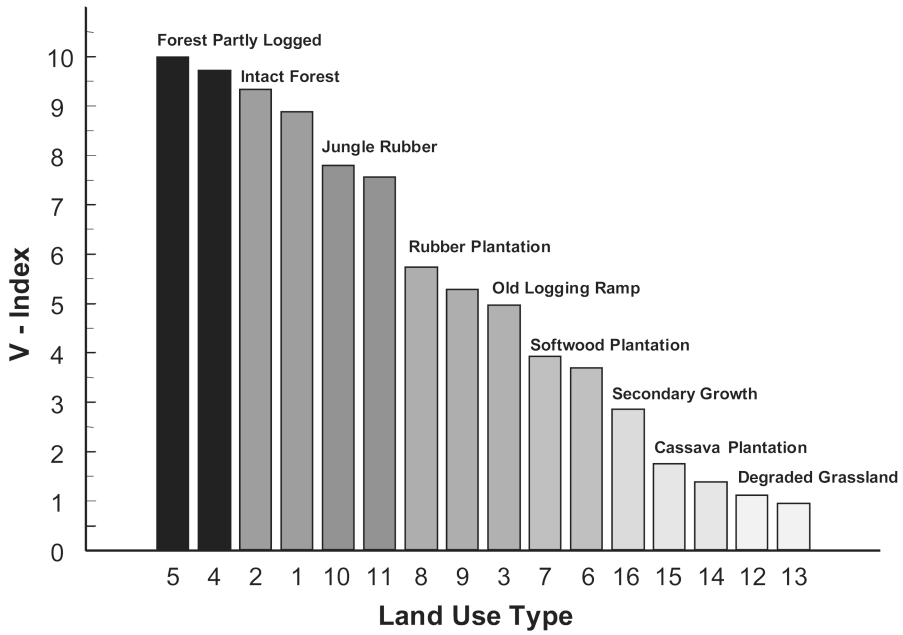


Figure 4.5 Land use types in Jambi, central Sumatra, ranked by vegetation index (V-index).

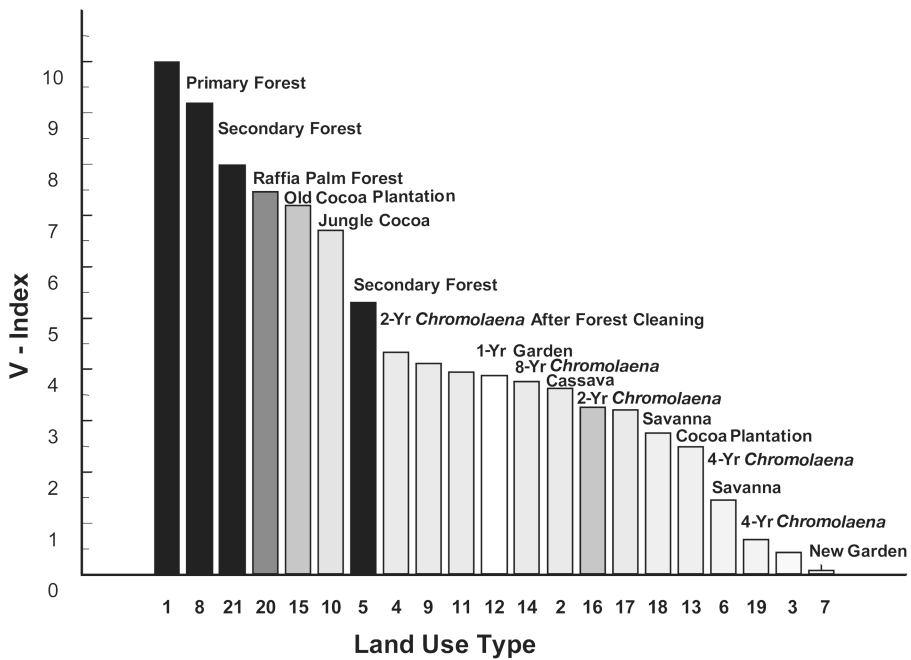


Figure 4.6 Land use types in Cameroon (Mbalmayo and Makam), ranked by vegetation index (V-index).

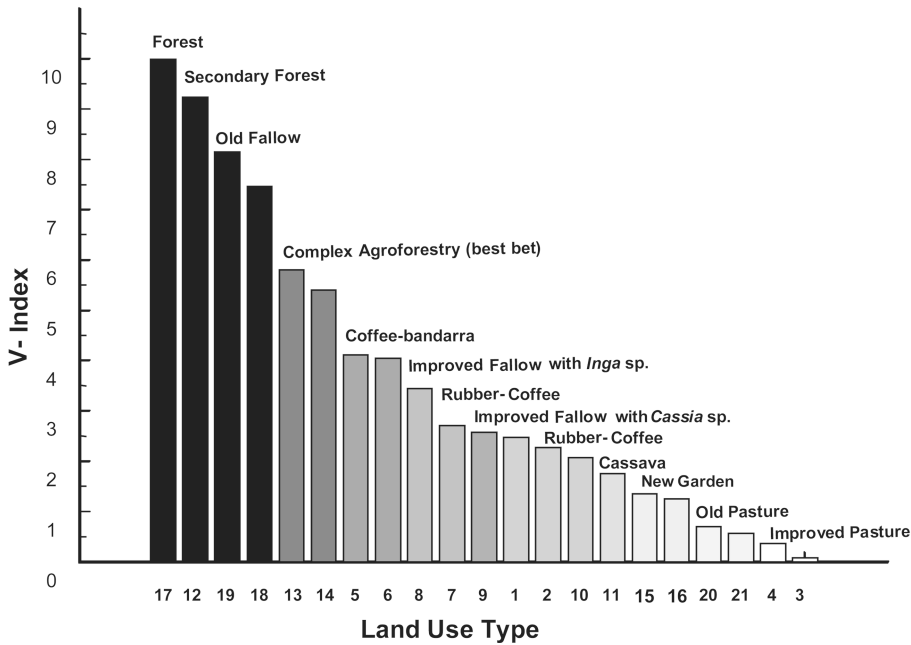


Figure 4.7 Land use types in Brazil (Rondônia and Acre), ranked by vegetation index (V-index).

Despite the improvements in plant-based biodiversity indicators recorded here, generalizations from these lowland studies must be made with due care because other preliminary studies (Gillison et al. 1996) indicate that similar predictive relationships may not hold in highland tropical environments. More robust predictive models therefore will require similarly calibrated surveys but within a wider array of ecoregional variation. Results emerging from parallel ASB studies in Thailand and South Sumatra (Gillison 2000b, 2000c) on the impacts of differing tenurial systems in coffee and oil palm management systems also support the concept that complex agroforests provide the best options for long-term management, despite the fact that short-term profit is greatest where capital exists to promote permanent, intensive farming systems.

There is increasing evidence that biodiversity, at least in certain circumstances (cf. those described by Tilman and Downing 1994), contributes to ecosystem stability and productivity, although this is not without debate (Hector et al. 1999; Huston et al. 2000; Loreau et al. 2001). In the present study, apparent links between agricultural productivity and profitability suggest that apart from fertilizer-enhanced, permanent, intensive cropping systems in which biodiversity is greatly reduced and short-term profitability increased, higher biodiversity is associated with higher soil nutrients and site productivity under longer fallows and under complex agroforests. Therefore a key challenge is to identify the principal biophysical and socioeconomic drivers of biodiversity and related profitability. Current ASB activities are pursuing this goal, seeking how best to identify and calibrate indicators that can be used directly in a policy

analysis matrix and in the formulation of appropriate policy interventions needed to sustain both economic growth and biological diversity.

CONCLUSION

The present studies demonstrate highly significant correlations between key plant and animal species, functional groups, vegetation structure, above-ground carbon, and key soil variables. These represent improvements on biodiversity predictors so far evaluated in other lowland, tropical, forested landscapes under slash-and-burn. Although a clearer understanding of the soil–plant–land use dynamic is needed to better manage ecosystem productivity, the study reveals potentially useful links between land use type and biodiversity. As shown in this and other studies in tropical forests, elements of vegetation structure can be used as a primary indicator of site productivity potential and biodiversity, and they can be significantly enhanced by the addition of readily observable plant functional types and key plant species. A best-bet option for managers of forested and agroforested lands is to maintain a mosaic of land cover types with a focus on complex agroforests rather than intensive monocropping. This strategy seeks to maximize the availability of ecological niches and thus biodiversity while sustaining an adequate soil nutrient base. Not only is this likely to enhance biodiversity, but it may also serve as an added buffer to unexpected variation in environmental and socioeconomic change. Incentives for adopting best-bet alternatives will be made more attractive to all stakeholders if these outcomes can be used to demonstrate more specific links between biodiversity and profitability.

APPENDIX

Plant Functional Attributes and Elements Used in the Plant Functional Type Grammar

Attribute	Element	Description
<i>Photosynthetic Envelope</i>		
Leaf size	nr	No repeating leaf units
	pi	Picophyll (<2 mm ²)
	le	Leptophyll (2–25 mm ²)
	na	Nanophyll (25–225 mm ²)
	mi	Microphyll (225–2025 mm ²)
	no	Notophyll (2025–4500 mm ²)
	me	Mesophyll (4500–18,200 mm ²)
	pl	Platyphyll (18,200–36,400 mm ²)
	ma	Macrophyll (36,400–18 × 10 ⁴ mm ²)
	mg	Megaphyll (>18 × 10 ⁴ mm ²)
Leaf inclination	ve	Vertical (>30° above horizontal)
	la	Lateral (±30° to horizontal)
	pe	Pendulous (>30° below horizontal)
	co	Composite

Chlorotype	do	Dorsiventral
	is	Isobilateral or isocentric
	de	Deciduous
	ct	Cortic (photosynthetic stem)
	ac	Achlorophyllous (without chlorophyll)
Morphotype	ro	Rosulate or rosette
	so	Solid 3-dimensional
	su	Succulent
	pv	Parallel-veined
	fi	Filicoid (fern; Pteridophytes)
	ca	Carnivorous (e.g., <i>Nepenthes</i>)

Supporting Vascular Structure

Life form	ph	Phanerotype
	ch	Chamaephyte
	hc	Hemicryptophyte
	cr	Cryptophyte
	th	Therophyte
	li	Liane
Root type	ad	Adventitious
	ae	Aerating (e.g., pneumatophore)
	ep	Epiphytic
	hy	Hydrophytic
	pa	Parasitic

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