

- Lampainen, J., Kuuluvainen, T., Wallenius, T.H., Karjalainen, L. & Vanha-Majamaa, I. 2004. Long-term forest structure and regeneration after wildfire in Russian Karelia. *J. Veg. Sci.* 15: 245-256.
- Leibundgut, H. 1957. Waldreservate in der Schweiz. *Schweiz. Zeitschr. f. Forstw.* 108: 417-421.
- Leibundgut, H. 1959. Über Zweck und Methodik der Struktur- und Zuwachsanalyse von Urwäldern. *Schweiz. Zeitschr. f. Forstw.* 110: 111-124.
- Leibundgut, H. 1962. *Richtlinien für die Aufnahme von Waldreservaten*. Unpubl. report. Institut für Waldbau, ETH Zurich, Zürich, CH.
- Leibundgut, H. 1966. *Die Waldpflege*. Haupt, Bern, CH.
- Leibundgut, H. 1984. *Unsere Waldbäume*. Huber, Frauenfeld, CH.
- Mayer, H. 1992. *Waldbau auf soziologisch-ökologischer Grundlage*. 4th ed. Gustav Fischer, Stuttgart, DE.
- Mölleken, H., Eckstein, D., Venne, H. & Scholz, F. 1994. Growth of spruce (*Picea abies* (L.) Karst.) as controlled by genotype and environment. *Dendrochronologia* 12: 23-32.
- Monserud, R.A. & Sterba, H. 1999. Modeling individual tree mortality for Austrian forest species. *For. Ecol. Manage.* 113: 109-123.
- Moons, K.G.M., Rogier, A., Donders, T., Steyerberg, E.W. & Harrell, F.E. 2004. Penalized maximum likelihood estimation to directly adjust diagnostic and prognostic prediction models for overoptimism: a clinical example. *J. Clin. Epidemiol.* 57: 1262-1270.
- Nishimura, N., Hara, T., Kawatani, M., Hoshino, D. & Yamamoto, S.-I. 2005. Promotion of species co-existence in old-growth coniferous forest through interplay of life-history strategy and tree competition. *J. Veg. Sci.* 16: 549-558.
- Nishimura, T.B. 2006. Successional replacement mediated by frequency and severity of wind and snow disturbances in a *Picea-Abies* forest. *J. Veg. Sci.* 17: 57-64.
- Pearce, J. & Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* 133: 225-245.
- Peduzzi, P., Concato, J., Kemper, E., Holford, T.R. & Feinstein, A.R. 1996. A simulation study of the number of events per variable in logistic regression analysis. *J. Clin. Epidemiol.* 49: 1373-1379.
- Peltola, H., Kellomäki, S., Väisänen, H. & Ikonen, V.-P. 1999. A mechanistic model for assessing the risk of wind and snow damage to single trees and stands of Scots pine, Norway spruce, and birch. *Can. J. For. Res.* 29: 647-661.
- R Development Core Team. 2006. *R: a language and environment for statistical computing*. R for windows 2.3.1. <http://www.R-project.org>.
- Reineking, B. & Schröder, B. 2006. Constrain to perform: Regularization of habitat models. *Ecol. Model.* 193: 675-690.
- Risch, A.C., Heiri, C. & Bugmann, H. 2005. Simulating structural forest patterns with a forest gap model: a model evaluation. *Ecol. Model.* 181: 161-172.
- Sachsse, H. 1984. *Einheimische Nutzhölzer und ihre Bestimmung nach makroskopischen Merkmalen*. Parey, Hamburg, DE.
- Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. 2005. ROCR: Visualizing the performance of scoring classifiers. R-package version 2.0-12. <http://rocr.bioinf.mpi-sb.mpg.de>
- Steyerberg, E.W., Harrell, F.E., Borsboom, G.J.J.M., Eijkemans, M.J.C.R., Vergouwe, Y. & Habbema, J.D.F. 2001. Internal validation of predictive models: efficiency of some procedures for logistic regression analysis. *J. Clin. Epidemiol.* 54: 774-781.
- Stone, C.J. & Koo, C.Y. 1985. Additive splines in statistics. In: *Statistical Computing Section ASA*, pp. 45-48. American Statistical Association, Washington, DC, US.
- Suarez, M.L., Ghermandi, L. & Kitzberger, T. 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *J. Ecol.* 92: 954-966.
- Temesgen, H. & Mitchell, S.J. 2005. An individual-tree mortality model for complex stands of Southeastern British Columbia. *West. J. Appl. For.* 20: 101-109.
- Theurillat, J.-P. & Guisan, A. 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Clim. Change* 50: 77-109.
- van Mantgem, P.J. & Stephenson, N.L. 2004. Does coring contribute to tree mortality? *Can. J. For. Res.* 34: 2394-2398.
- Waring, R.H. & Pitman, G.B. 1985. Modifying logdepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66: 889-897.
- Wunder, J., Bigler, C., Reineking, B., Fahse, L. & Bugmann, H. 2006. Optimisation of tree mortality models based on growth patterns. *Ecol. Model.* 197: 196-206.
- Wyckoff, P.H. & Clark, J.S. 2000. Predicting tree mortality from diameter growth: a comparison of maximum likelihood and Bayesian approaches. *Can. J. For. Res.* 30: 156-167.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants XI). *J. Biol. Osaka City Univ.* 14: 107-129.

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## The RAINFOR database: monitoring forest biomass and dynamics

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### Abstract

**Problem:** Data from over 100 permanent sample plots which have been studied for 10-20 years need a suitable system for storage which allows simple data manipulation and retrieval for analysis.

**Methods:** A relational database linking tree records, taxonomic nomenclature and corresponding environmental data has been built in MS Access as part of the RAINFOR project.

**Conclusion:** The database allows flexible and long-term use of a large amount of data: more than 100 tree plots across Amazonia, incorporating over 80 000 records of individual trees and over 300 000 total records of tree diameter measurements from successive censuses. The database is designed to enable linkages to existing soil, floristic or plant-trait databases. This database will be a useful tool for exploring the impact of environmental factors on forest structure and dynamics at local to continental scales, and long term changes in forest ecology. As an early example of its potential, we explore the impact of different methodological assumptions on estimates of tropical forest biomass and carbon storage.

**Keywords:** Amazon; Data management; Ecoinformatics; Long-term; Plot; Tropical.

**Abbreviations:** RAINFOR = The Amazon Forest Inventory Network; DBH = Diameter at breast height; POM = Point of measurement; CTFS = Centre for Tropical Forest Science; ABG = Above-ground biomass; AVDL = Applied Vegetation Dynamics Laboratory.

### Introduction

The Amazon Forest Inventory Network (RAINFOR), an international project established to monitor large-scale patterns of forest structure and dynamics across Amazonia (Malhi et al. 2002), has collected and collated inventory data from a large number of forest plots. We have recently developed a database to integrate data from over 100 permanent sample plots across the Amazon which have typically been studied for 10-20 years each, some as long as 30 years.

A primary aim of RAINFOR is to monitor forest biomass and dynamics across Amazonia in a coordinated fashion in order to understand their relationships with soil and climate. The network examines the continental-scale relations between forest structure, dynamics and environmental factors, and explores how the ecology of these forests may change over time. For example, initial publications have concentrated on spatial and temporal patterns of biomass, wood productivity and tree mortality, recruitment and growth rates (Malhi et al. 2002; Baker et al. 2004a, b; Lewis et al. 2004; Malhi & Phillips 2004; Phillips et al. 2004).

It is clear that the projects' aims cannot be fully achieved without a powerful database to collate, sort, and extract data for analysis. The database would need to be able to handle data from repeated measures through time and store information on the diameter at breast height (DBH) of individual trees, tree status and tree death. Other ecological databases exist, but none have a structure to suit the requirements of the RAINFOR project. For example, the AVDL (Applied Vegetation Dynamics Laboratory) (Le Duc et al. 2007, this issue) database is designed to handle data from repeated measures through time, but it is also designed to handle metadata generated from different complex experiments and structured surveys (Le Duc et al. 2007, this issue) – this level of information is not required in the RAINFOR database as the field protocol for each plot and re-census is standardised. Additionally these databases, and other available web-based phytosociological databases such as VEGBANK (Jennings et al. 2004) and TURBOVEG (Hennekens & Schaminée 2001), are

not suitable for records of tree diameter, status or death modes, information which is key to the RAINFOR research agenda. VEGBANK and TURBOVEG are more suitable for describing plant communities rather than recording individual trees.

It is expected that over the coming years the RAINFOR database will: (1) enable increasingly complex questions concerning macro-ecology and ecological change to be tackled, (2) link with existing and future soil, floristic, climatic and trait databases, (3) be extended to the all tropical regions and possibly worldwide. Specific examples of how the database is being used include: to test for recent floristic change in old-growth Amazonia forests; to assess patterns of alpha diversity across Amazonia; to develop bioclimate envelopes for western Amazonia taxa; to calculate mortality and growth rates for comparison between taxa; as a means to assess how mode of mortality varies with climate, soil and species composition; and as a tool to support development of spatially-explicit models of forest dynamics. In addition, when used in conjunction with a functional traits database also being developed, it will help answer questions on functional change across the Amazon, and how these vary depending on environmental variables. The research that can potentially be enabled by the RAINFOR database spans a vast thematic and geographic range.

The RAINFOR field protocol and analytical treatments are already published (see Baker et al. 2004; Phillips et al. 2004; Lewis et al. 2006; <http://www.geog.leeds.ac.uk/projects/rainfor/>). The RAINFOR database is being used as an important scientific tool within the project. Although the complexity of handling data from so many participants means it is currently not possible to provide public access, RAINFOR actively seeks new collaborations and encourages the use of existing data by all participants.

Here we present the general structure of this new database on forest dynamics and floristics as well as environmental information, which could serve as a template for further applications in forest ecology and other vegetation types. Finally, we discuss the limitations of the project and further possible implementations.

Updating and improving the taxonomic records is an ongoing process. In the 'CollectionNo' table we include a herbarium voucher number that belongs to each individual tree in the database. This allows the integration of updated taxonomic information from TROPICOS through a standard query as taxonomic science improves.

## Methods

### The data

RAINFOR has access to data from permanent sample plots, where every tree is identified, labelled and tracked through time. Typically plots comprise of information on all trees  $\geq 10$  cm diameter at a reference height of 1.3 m, unless otherwise stated (e.g. if a tree has a buttress). Most plots are 1 ha in size, and there are > 100 non-contiguous plots, each with 2-20 censuses. For each plot there is information on the taxonomy of the trees, the diameter of each tree at each census, whether a tree has died, and if so, how it died. In total there are records for > 80 000 individual trees and > 300 000 total records of tree diameter measurements from successive censuses. Previously, the data from each plot was all stored in different spreadsheets and in different formats. It was therefore difficult to compare the data from the different plots. As the number of plots and censuses increased the need for a database to extract the appropriate data for analyses became increasingly necessary.

### Sorting the data

All data were standardised according to RAINFOR protocols before being entered into the database. In addition tree records originated from different geographical areas and time periods, taxonomic harmonisation was also necessary. We used SALVIAS TaxonScrubber (Boyle 2004) for standardising species names. This is a stand-alone application for automated standardization of taxonomic names that has been developed specifically to efficiently standardise species lists to a common format. It matches names to a standard list of validly published names and standardises all family names to match taxonomic concepts and spellings of the Missouri Botanical Garden's TROPICOS database (<http://mobot.mobot.org/W3T/Search/vast.html>). TROPICOS is the world's largest database of plant information, with special emphasis on the neotropics. In a small minority of cases this included the matching of scientific and vernacular names through rigorous checking with herbaria records, local field experts and local floras.

Updating and improving the taxonomic records is an ongoing process. In the 'CollectionNo' table we include a herbarium voucher number that belongs to each individual tree in the database. This allows the integration of updated taxonomic information from TROPICOS through a standard query as taxonomic science improves.

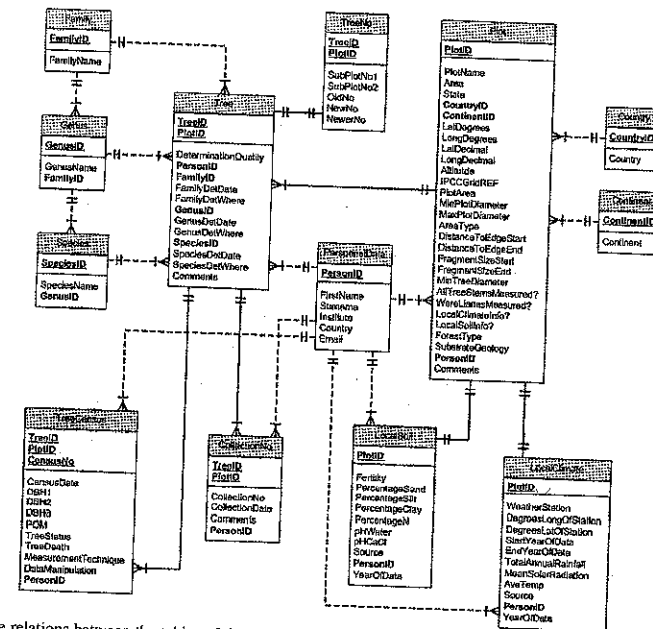


Fig. 1. Schema of the relations between the tables of the RAINFOR database, with a list of their respective fields. Primary keys are underlined, items in bold are required. Solid lines represent links between primary keys. The relationships between TreeNo and Tree, Plot and LocalSoil, and Plot and LocalClimate are one to one. All other relationships are one to many. The type of relationship is shown by the symbols: '+' = many and '#' = one.

### The database structure

The database consists of 13 linked tables (Fig. 1). The PersonnelData table is linked to most other tables. It contains the name and contact details, where appropriate, of the people involved in each step from the fieldwork, collection of samples, identification, providing environmental data, and data management in the UK.

The Plot table corresponds to each permanent sample plot in the field, each with a unique identification code. This table is designed so that data from different groups of plots such as, from a specified country or above a certain altitude, can be easily extracted. It also contains plot-level information, including plot size, substrate geology, and the dates of plot establishment and the most recent census, as well as the forest type, such as *terra firme*, seasonally flooded or swamp forest and the size of the fragment of forest where it is located, if appropriate.

In addition to the PersonnelData table, the Plot table is linked directly to two environmental tables. One contains information on the soil (LocalSoil) at each plot if

available and the other on the climatic (LocalClimate) data at each plot. The Plot table is also linked to the Tree table. Each tree in a plot is given an identification number, which, together with the plot identification code uniquely identifies each tree in the database. This table contains tree-level information including the codes for family, genus and species names for each tree and where the determination was carried out (in the field, in the herbarium or in the field and confirmed in the herbarium). Family, genus and species have all been coded and are contained in separate tables. Currently, in total there are > 2500 identified species in >100 families.

The TreeNo table contains all the original field numbers and subplots and makes comparison of field record sheets and the database efficient. This is important for correcting potential errors in the dataset.

The final table linked to the tree table is the TreeCensus table. The TreeCensus table has three primary keys – plot ID, tree ID and census number – which when used together identify a particular tree in a specific census. The tree census table contains the measured diameter

of each tree and the above-ground height at which it was measured, termed the point of measurement, POM. POMs sometimes have to be moved, as buttresses can develop on a stem and expand over time in many tropical trees. Hence, the database includes fields that standardise the diameter measurement to both the initial and the new POM (from the ratio of diameters at both POMs), which allows maximum flexibility in how the data can be subsequently analysed. Records where POM changes have occurred can be removed or utilised using a variety of methods to account for POM changes, for example, to remove spurious negative growth rates from individual stems when POMs have been changed, by utilising the field where growth is standardised to the initial or new POM. The tree status field codes for the state of the tree while it is alive. For example, these codes describe whether the tree is leaning or broken. Overall, there are 21 such codes which can be used in combination to describe a tree. The tree death field describes four aspects of tree death; how (e.g. broken trunk, or uprooted); whether it died alone or with other trees; whether it was the 'killed' or the 'killer tree' in a mortality event; and the most likely cause of death (e.g. disease, lightning strike).

#### Data entry and quality assurance

Data can be added in two ways: firstly bulk data from spreadsheets can be imported into the database. Secondly, forms have been designed which are useful for adding small amounts of data, or updating previously entered records. Both methods of data entry are simple and very little training is required to perform these tasks. Separate forms are used for updating tree (Fig. 2A) and plot data (Fig. 2B). Updating tree data is occasionally necessary, for example in cases where a tree is presumed dead during one census having not been found but is re-discovered in the next census.

In addition to in-field and data-entry quality control procedures, two database quality-control procedures further minimise the potential for errors to enter the data. Firstly, controls are set in each field (column) of every table so illegal data can not be entered (e.g. text in a numbers field, numbers outside a credible range, non-standard species names). Secondly after entering data several queries are run to check for errors. For example we calculate the total number of alive stems in a census, the number of stems that died and were recruited between census dates, the number of alive stems in the new census, and check that there is an internally consistent number of stems (Table 1).

#### Data extraction

Data can be extracted by one of two methods: firstly, using standard queries that have been pre-programmed, some static and some allowing user defined parameters, or secondly by user programmed queries. The first method requires little or no prior knowledge of the database structure, while the second requires greater understanding of the database but allows greater flexibility in the specific data extracted. Each pre-programmed query is accompanied by notes explaining the exact nature of the data that they extract. Extracted data can be imported into a spreadsheet or statistical package.

An example of a standard query with user defined parameters is one to calculate above ground biomass (AGB) per plot based on three different equations, the output from this query is shown in Table 2. The user can define which plots they wish to be included in the query and which census number or census date. The results from the query shown here cover the first census of each plot (Table 2 and Fig. 3). The calculation of biomass per plot is important when trying to quantify changes over time in carbon storage of forests, which is important for understanding potential impacts on global climate change (Prentice et al. 2001). This query calculates biomass using three different allometric equations. Equations 1 and 2 are based on the same tree harvest data (315 trees, harvested as part of the BIONTE project, near Manaus, Brazil); Eq. 1 calculates AGB on a per stand basis (Phillips et al. 1998), Eq. 2 calculates AGB on a per stem basis (Chambers et al. 2001). Eq. 3 was derived from an independent set of tree diameter and mass data of 378 trees (Chave et al. 2001). The equations used in the query are:

$$AGB = 0.6 * (66.92 + (16.85 * BA)) \quad (1)$$

$$AGB = \sum_i \exp(0.33(\ln D_i) + 0.933(\ln D_i)^2 - 0.122(\ln D_i)^3 - 0.37) \quad (2)$$

**Table 1.** Output of the standard query to check for errors in census data. A = number of trees alive in previous census; B = trees died by new census; C = trees recruited by new census; D = number of trees alive in new census; check, D = A - B + C, can return true or false, if false there is a mistake in the data.

Plot ID	A	B	C	D	Check
CUZ-01	333	67	59	525	True
CUZ-02	539	56	75	558	True
CUZ-03	495	48	50	497	True
CUZ-04	599	91	83	591	True

$$AGB = \sum_i \exp(2.42(\ln D_i) - 2.00) \quad (3)$$

Where BA = basal area, calculated as  $\pi(D_i/2)^2$

$D_i$  is the diameter of a tree  $i$  and  $n$  is the number of trees per plot.

Three equations are used because, although equations that calculated AGB on a per stem basis are often presumed to be more accurate than stand-level basal area, sometimes the only published data is at stand-level, so it is useful to be able to derive biomass from stand level data.

Although the three equations give biomass estimates that are strongly correlated ( $r^2$  varies from 0.854 for Eqs. 2 and 3, to 0.950 for Eqs. 1 and 2) there are differences in the estimated values (Fig. 3). For each possible set of two equations, biomass estimates were linearly regressed. The estimated slopes were tested to determine whether they significantly differed from one and the intercepts

**Table 2.** A sample of the output of a standard query that calculates biomass per plot (full output included 112 plots). Biomass estimates are in units of  $Mg \cdot ha^{-1}$ .

PlotCode	Eq1	Eq2	Eq3
ACL-01	288.21	352.62	324.30
AGJ-01	342.26	354.07	233.13
ALM-01	160.83	181.65	148.14
ALP-11	289.22	324.89	295.42
ALP-12	252.29	291.77	283.71
ALP-21	269.51	306.78	299.44
ALP-22	252.65	279.40	241.07
ALP-30	227.87	264.11	260.67
BDF-03	288.47	332.00	338.72
BDF-04	276.15	307.96	332.33
BDF-05	251.97	280.38	298.02
BDF-06	255.65	285.44	299.49
BDF-07	290.14	334.58	366.99
BDF-08	282.92	325.53	337.30
BDF-09	303.53	356.91	389.15

**Fig. 2.** Form for entering and updating A. tree data. B. Plot data, within the RAINFOR database.

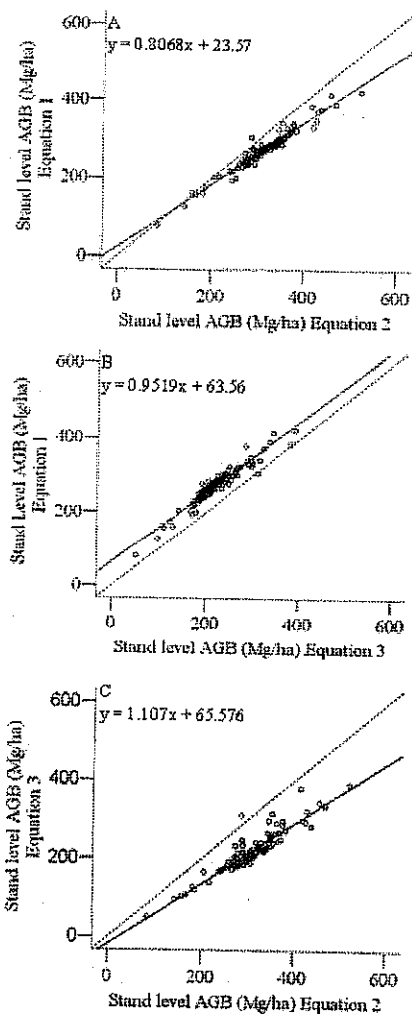


Fig. 3. The relationship between estimates of AGB calculated per stem and per plot. Dotted lines show a one to one relationship, through the origin. A. Results from Eq. 1 vs. Eq. 2. B. Results from eq. 1 vs. Eq. 3. C. Results from Eq. 2 vs. Eq. 3.

**Table 3.** *t*-distribution values and probabilities of significant differences, calculated following (Sachs 1984). \* =  $P \leq 0.02$ , \*\* =  $P \leq 0.001$ ;  $df = 110$ .

Equation pairs	Intercept different from 0	Slope different from 1
1 v 2	$t = 4.16$ **	$t = 10.73$ **
1 v 3	$t = 10.38$ **	$t = 1.78$
2 v 3	$t = 6.52$ **	$t = 2.43$ *

tested to determine if they were significantly different from zero (Sachs 1984) (Table 3).

Although the slope from the comparison of equations 1 and 3 does not depart significantly from one, the intercept is significantly different from zero (Table 3). This shows that the AGB estimates produced by the two equations are different by a constant value, with Eq. 3 providing lower estimates than Eq. 1 (Fig. 3B). The slopes produced from the comparison of Eqs. 1 and 2, and Eqs. 2 and 3 were significantly different from Eq. 1 (Table 3). This shows that the difference in output of these equations changes as biomass values change and not by an absolute value (Fig. 3A, C). Given these inconsistencies between the different models, including the three equations in the database allows users to assess the sensitivity of their conclusions concerning patterns of biomass and biomass change to uncertainty in the underlying allometric relationship (Chave et al. 2004).

### Discussion and Conclusion

In developing the RAINFOR database it has been necessary to tackle several practical issues concerning the organisation of heterogeneous data: the plots contain tree records from two to 25 censuses, vary from 0.2 ha to 10 ha in size, and include multiple census dates from as early as the 1960s to 2006, over which time individual trees may be recruited, grow, have their point of measurement moved, and die. In addition, we need to track dynamic and changing nomenclature attributes, as well as harmonise the floristic data to common standards.

The RAINFOR database is a product of the large collaborative efforts of researchers working across Amazonia and beyond. It is intended to permit efficient and accurate storage of inventory data to provide information to these researchers to address questions about the structure and functioning of Amazonian forests. Developing collaborative networks of researchers is an increasingly important theme of research in tropical forests (e.g. Corlett & Primack 2006). The spatially distributed network of many long-term monitoring sites that RAINFOR maintains has led to insights into the changing

ecology of tropical forests (Baker et al. 2004a; Lewis et al. 2004; Phillips et al. 2004). The Centre for Tropical Forest Science (CTFS) large-scale plot network has led to fundamental insights into the processes maintaining tropical forest diversity (Losos & Leigh 2004), and the Amazon Tree Diversity Network ([http://www.bio.uu.nl/~herba/Guyana/Amazon\\_plot\\_network/Introduction.htm](http://www.bio.uu.nl/~herba/Guyana/Amazon_plot_network/Introduction.htm); ter Steege et al. 2003) has drawn together data from several hundred single census plots to improve our understanding of patterns of diversity and composition of Amazonian forests. Development of the RAINFOR database is indeed itself indebted to the existence of the TROPICOS database at the Missouri Botanical Garden (<http://mobot.mobot.org/W3T/Search/vast.html>), the SALVIAS project (<http://www.salvias.net/pages/index.html>) and the CTFS Neotropical Tree Species Checklist (<http://ctfs.si.edu/neotropicaltree/>), themselves all products of major research collaborations. By uniquely drawing together numerous long-term inventory data from a wide geographical area, including plots in a wide range of habitats, and some of the longest running monitoring sites in Amazonia, the RAINFOR database will enable further collaborative research and provide an novel resource for addressing pressing questions about the current and future ecology of tropical forests in a rapidly changing world (Lewis 2006).

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### References

- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Killeen, T., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patiño, S., Pitman, N.C.A., Silva, N. & Vásquez Martínez, R. 2004a. Increasing biomass in Amazonian forest plots. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 359: 353-365.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Killeen, T., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patiño, S., Pitman, N.C.A., Silva, N. & Vásquez Martínez, R. 2004b. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biol.* 10: 545-562.
- Boyle, B.L. 2004. *TaxonScrubber Version 1.2*. The SALVIAS Project, <http://www.salvias.net>. (Accessed [05/04/2005]).
- Chambers, J.Q., dos Santos, J., Ribeiro, R.J., Higuchi, N. 2001. Tree damage, allometric relationships, and above-ground

- net primary production in a central Amazon forest. *For. Ecol. Manage.* 152: 73-84.
- Chave, J., Riera, B. & Dubois, M.A. 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *J. Trop. Ecol.* 17: 79-96.
- Chave J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. 2004. Error propagation and scaling for tropical forest biomass estimates. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 359: 409-420.
- Corlett, R.T. & Primack, R.B. 2006. Tropical rainforests and the need for cross-continental comparisons. *Trends Ecol. Evol.* 21: 104-110.
- Hennekens, S.M. & Schamineé, J.H.J. 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *J. Veg. Sci.* 12: 589-591.
- Jennings, M., Faber-Langendoen, D., Peet, R., Loucks, O., Glenn-Lewin, D., Damman, A., Barbour, M., Pfister, R., Grossman, D., Roberts, D., Tart, D., Walker, M., Talbot, S., Walker, J., Hartshorn, G., Waggoner, G., Abrams, M., Hill, A. & Rejmánek, M. 2004. *Guidelines for describing associations and alliances of the U.S. National Vegetation Classification*. The Ecological Society of America, Vegetation Classification Panel. (Download available at: [http://vegbank.org/vegdocs/panel/NVC\\_guidelines\\_v4.pdf](http://vegbank.org/vegdocs/panel/NVC_guidelines_v4.pdf).)
- Le Duc, M.G., Yang, L. & Marrs, R.H. 2007. A database application for long-term ecological field experiments. *J. Veg. Sci.* 18: 509-516.
- Lewis, S.L. 2006. Tropical forests and the changing Earth System. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 361: 195-210.
- Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D., Silva, N., Terborgh, J., Torres Lezama, A., Vásquez Martínez, R., Brown, S., Chave, J., Kuebler, C., Núñez Vargas, C. & Vinceti, B. 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 359: 421-436.
- Losos, E. & Leigh, E.G. 2004. *Tropical forest diversity and dynamics: findings from a large scale plot network*. University of Chicago Press, Chicago, IL, US.
- Malhi, Y. & Phillips, O.L. 2004. Tropical forests and global atmospheric change: a synthesis. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 359: 549-555.
- Malhi, Y., Phillips, O.L., Lloyd, J., Baker, T.R., Wright, J., Almeida, S., Arroyo, L., Frederiksen, T., Grace, J., Higuchi, N., Killeen, T., Laurance, W.F., Leão, C., Lewis, S., Meir, P., Monteagudo, A., Neill, D., Núñez Vargas, P., Panfil, S., Patiño, S., Pitman, N., Quesada, C.A., Ruelas-Ll. A., Salomão, R., Saleska, S., Silva, N., Silveira, M., Sombroek, W.G., Valencia, R., Vásquez Martínez, R., Vieira, I.C.G. & Vinceti, B. 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). *J. Veg. Sci.* 13: 439-450.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Núñez Vargas P., Vásquez Martínez, R., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S. & Grace, J. 1998. Changes in the carbon balance of tropical forests: evidence from long term plots. *Science*. 282:439-442.

- Phillips, O.L., Baker T.R., Arroyo, L., Higuchi, N., Killeen, T., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D., Núñez Vargas, P., Silva, N., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Palacios, W., Patiño, S., Pitman, N., Olivier, J., Quesada, C.A., Saldias, M., Torres Lezama, A. & Vinceti, B. 2004. Pattern and process in Amazon tree turnover, 1976-2001. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 359: 381-407.
- Prentice, I.C. (and 60 others) 2001. The carbon cycle and atmospheric carbon dioxide. In: IPCC (ed.) *Climate change 2001: the scientific basis*, pp. 183-197. Cambridge University Press, Cambridge, UK.
- Sachs L. 1984. *Applied Statistics: A handbook of techniques*. 2nd. ed. Springer-Verlag, New York, NY, US.
- Ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van der Hout, P., Daly, D.C., Silveira, M., Phillips, O.L., Vasquez, R., Van Andel, T., Duivenvoorden, J., De Oliveira, A.A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Vargas, P.N., Mogollon, H. & Morawetz, W. 2003. A spatial model of tree alpha-diversity and tree density for the Amazon. *Biodivers. Conserv.* 12: 2255-2277.

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## Predictability, contingency, and convergence in late succession: Slow systems and complex data-sets

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### Abstract

**Questions:** Are community dynamics in old-growth forests predictable? Convergent? Equilibrial? Are answers to these questions dependent on temporal and spatial scale? How can complex, long-term observational data be used most powerfully to address these questions?

**Location:** 100-ha tract of old-growth cool-temperate forest in northern Michigan, USA.

**Methods:** Woody stems were measured, on 243 permanent plots, several times, at varying intervals and intensity, over 70 years. A range of visualization tools and multivariate statistics were used to extract patterns and address questions posed.

**Results:** This ancient forest is not equilibrial; compositional trends suggest that changes are competitively driven and reflect long-lasting effects of disturbance. Predictability of community change varies across environmental gradients, with interval between samples, with spatial scale, and depending on type of predictability being assessed. Plot trajectories in species-space and changes in diversity suggest successional convergence within some habitats, but not across habitats. Dynamics are strongly structured at the scale of 'habitat-patches'.

**Conclusions:** Appropriate address of questions about community dynamics requires observational data of appropriate spatial and temporal scale and resolution. Powerful use of such data-sets calls for data-management and analysis tools that are robust with respect to irregularities in design and data structure. While interpretation of long-term descriptive data is challenging, appropriate analyses cast light on late successional dynamics, allowing address of models and hypotheses that are otherwise difficult to test.

**Keywords:** *Acer saccharum*; *Betula alleghaniensis*; Ecoinformatics; *Fagus grandifolia*; Hemlock-northern hardwood forest; Old-growth forest; Permanent plot; *Thuja occidentalis*; *Tsuga canadensis*.

**Nomenclature:** Gleason & Cronquist (1991).

**Abbreviation:** RNA = Dukess Research Natural Area.

### Introduction

Despite a long history of debate about dynamics of late-successional forests (Are they stable? Equilibrial? Structured by ecological interactions? 'Neutrally' assembled?), opportunities for rigorous testing of competing hypotheses are rare. Studies employing space-for-time substitutions (for example, chronosequences and extrapolations from spatial pattern of canopy gaps and regeneration) are frequent, but involve risky assumptions about history (Pickett 1989). Paleoecology offers long-term perspective, but only rarely provides spatial and temporal resolution requisite for understanding stand-scale dynamics (but see Arseneault 2004; Parshall 1995). Dendrochronology and stand reconstruction can provide great detail and resolution at the scale of centuries (e.g. Henry & Swan 1974; Abrams et al. 1998) but are extremely labor-intensive. Simulation models can provide both long-term perspectives and high resolution (see Busing & Maily 2004), but require empirical data for assessment of accuracy.

While combinations of such approaches can be powerful (e.g. Bakker et al. 1996; Baker et al. 2002), they all, ultimately, involve assumptions that can be most rigorously tested only with longitudinal data. Planned longitudinal studies of slow, late-successional communities, however, are logistically prohibitive. Consequently, strong empirical evidence concerning dynamic properties of communities is generally from constructed or early-successional communities of short-lived species. Quantitative, plot-based studies of temperate forest vegetation spanning more than a decade are rare (Woods 2000a, b), and even fewer concern late-successional stands (but see Franklin & DeBell 1988; Harcombe et al. 2002). Thus, current understanding of such vegetation retains a large anecdotal element.

This situation places a high premium on exploitation of historical data sets, especially those from permanent plots (Bakker et al. 1996). However, powerful use of historical data can be constrained by special problems of information management and analysis. Initial measurements in historical data-sets are likely to have been structured for purposes other than assessment of