Tropical Ecosystem and Soil Development

Joost van Haren
Ecology 596L
09/03/10
Ecosystem biomass strongly dependent on soil


$R^2 = 32.3\%, \ P = 0.0002$

$R^2 = 38.4\%, \ P < 0.0001$

Manaus, BDFF plots
Ecosystem growth strongly dependent on soil

**Malhi, LBA meeting 2008**

**Biomass carbon increment (t C/ha/yr)**

- Old oxisols
- Spodosol/psamment
- Ultisols
- Younger oxisols
- Crystalline shield
- Holocene alluvium
- Older alluvium
- Inceptisols/andisols

Increasing fertility

Malhi, LBA meeting 2008
Main questions I’ll address

• How do necessary ecosystem ingredients (C, H, O, N, P, S, and micro nutrients) get into organisms?

• What factors influence soil formation?
  – Effect of time, parent material, and land-use change on soil nutrient content and ecosystem development
  – How does soil nutrient content vary over time

• Do soils influence tree diversity or do plants influence soil evolution?

• Final grab bag:
  – influence of land use change and fertilization
  – Do plant species really care what nutrient source is available?
  – Why do so many legumes not fix nitrogen?
How do necessary ecosystem ingredients get into above ground organisms?

**Organisms need:**

- **Carbon**
- **Nutrients**
  - N
  - S
  - P
  - Cations ($\text{Ca}^+$, $\text{Mg}^+$, $\text{K}^+$, ...)
  - Micro nutrients (Fe, Cu, Mn, Zn, ...)
- **Water**

**Ultimate source**

- Atmosphere ($\text{CO}_2$) (via biological photosynthesis)
- Atmosphere ($\text{N}_2$ is 80%) (via biological fixation and deposition)
- Atmosphere ($\text{SO}_4^{2-}$-wet deposition)
- Parent rock material (via chemical weathering)
- Atmospheric deposition (from dust storms & fire)
- Ocean (via evaporation & recon-densation as precip.)
How do necessary ecosystem ingredients get into above ground organisms?

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- **Nutrients**
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  - Micro nutrients (Fe, Cu, Mn, Zn, ...)
- **Water**
- **ENERGY**

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- **Parent rock material** (via chemical weathering)
- **Atmospheric deposition** (from dust storms & fire)
- **Ocean** (via evaporation & recon-densation as precip.)
- **Sun** and chemical reactions
How do necessary ecosystem ingredients get into soil/below ground organisms?

<table>
<thead>
<tr>
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<th>Ultimate source</th>
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<td>Carbon</td>
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<td></td>
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<td>- Micro nutrients ($Fe$, $Cu$, $Mn$, $Zn$, ...)</td>
<td>Ocean (via evaporation &amp; recon-densation as precip.)</td>
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<td>Sun and chemical reactions</td>
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<tr>
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<td></td>
</tr>
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</table>
What are nutrients used for in plants?

- **N**: chlorophyll, nucleic acids (DNA, RNA), amino acids, enzymes, proteins, vitamins, and hormones
- **P**: nucleic acids (DNA, RNA), phospholipids (cell wall), adenosine triphosphate (ATP, energy storage and transfer), and phosphopyridine nucleotides (NAD\(^+\), NADP\(^+\))
- **S**: proteins, polysaccharides, vitamins, and hormones
- Metal micronutrients: enzymes
Main questions I’ll address

Soil nutrient dynamics

• How do necessary ecosystem ingredients (C, H, O, N, P, S, and micro nutrients) get into organisms?

• What factors influence soil formation?
  – Effect of time, parent material, and land-use change on soil nutrient content and ecosystem development
How is soil generated from rocks?

Weathering

Largely undecomposed organic debris (leaves, etc.)
Partly decomposed organic debris
Dark horizon of mixed mineral and organic matter with a lot of biological activity
Light horizon of maximum eluviation
Transitional to B but more like A
Transitional to A but more like B
Maximum amounts of clay minerals or oxides and organic matter
Transitional to C but more like B
Weathered parent material
Layer of rock beneath soil

FIGURE 11-5. The designation of horizons for a hypothetical soil profile that could represent a forest soil in a cool, moist climate.
Soil Formation

<table>
<thead>
<tr>
<th>Independent variables or soil-forming factors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate</td>
</tr>
<tr>
<td>Organisms</td>
</tr>
<tr>
<td>Topography</td>
</tr>
<tr>
<td>Parent material</td>
</tr>
<tr>
<td>Time</td>
</tr>
</tbody>
</table>

\[ s = f'(c_l', o', r', p, t) \]  

\( s \) is any soil variable such as pH, texture, porosity, Ca content, etc.  

Jenny 1941
Soil Formation

<table>
<thead>
<tr>
<th>Independent variables or soil-forming factors</th>
<th>Climate</th>
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<tr>
<td></td>
<td>Organisms</td>
<td>(o')</td>
<td></td>
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<tr>
<td></td>
<td>Topography</td>
<td>(r')</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Parent material</td>
<td>(p)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>(t)</td>
<td></td>
</tr>
</tbody>
</table>

All important in ecosystem development and diversity

\[ s = f'(cl', o', r', p, t) \]  

\( s \) is any soil variable such as pH, texture, porosity, Ca content, etc.  

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Jenny 1941
Tropical soil and ecosystem development over time: example from Hawaii
Hawaii as a model of ecosystem development over 4.1 Myrs

Hawaiian islands are extraordinary natural laboratory allowing chronosequences in which (ideally) all factors except time are held constant

Chadwick et al. (1999)
None of the native Hawaiian tree species are legumes. N trend without legume trees!
Chadwick et al. 1999: Soil evolution over time

- Ca drops off through time (main source is parent rock)
- Importance of atmospheric deposition as source increases

- P drops off through time (main source is parent rock)
- In oldest soils, most is from atmospheric dust (a source likely 10X stronger in ice ages than interglacials), though bird poop cannot be excluded
Hawaii as a model of ecosystem development over 4.1 Myrs

Fertilization Experiments on Chronosequence

Tree growth

Treatment: Control N P N+P

Young sites N-limited
Middle sites jointly-limited
Old sites P-limited

Chadwick et al. (1999)
Vitousek & Farrington (1997)
Ecosystem development

How do young and old soils differ?

• Young soils:
  – should be rich in rock-derived elements (P, cations)
  – should be poor in atmospherically derived elements and those from organic matter degradation

• Older soils:
  – should be poor in rock-derived elements, due to leaching and soil erosion
  – should be richer in elements from atmospheric deposition and those from organic matter degradation
Based on the Hawaii story what would you expect for the nutrient status of Amazon basin soils?
Based on the Hawaii story what would you expect for the nutrient status of Amazon basin soils?

End of Miocene
10-15 million years ago

End of Pleistocene
1-3 million years ago

Present

Kaolinite
Gibbsite
Hematite
Quartz
Rapid N-recovery in secondary forest

N-recovery secondary forests is rapid due to high levels of N-fixation

Secondary forests are mainly on old soils (P limited) and years of agriculture deplete soil N.
Spatial variability soil texture and fertility: Influence of topography

Livingston et al. 1988

pH = 3.7
N = 0.07%
NH$_4^-$-N = 2.5 μg g$^{-1}$
NO$_3^-$-N = 0.5 μg g$^{-1}$
BM N = 27.9 μg g$^{-1}$
Min = 7.6 μg g$^{-1}$
NO$_3$ prod = 6.1 μg g$^{-1}$

pH = 4.0
N = 0.13%
NH$_4^-$-N = 2.7 μg g$^{-1}$
NO$_3^-$-N = 1.4 μg g$^{-1}$
BM N = 72.3 μg g$^{-1}$
Min = 14.1 μg g$^{-1}$
NO$_3$ prod = 15.4 μg g$^{-1}$

pH = 4.0
N = 0.22%
NH$_4^-$-N = 4.2 μg g$^{-1}$
NO$_3^-$-N = 1.3 μg g$^{-1}$
BM N = 119.6 μg g$^{-1}$
Min = 19.3 μg g$^{-1}$
NO$_3$ prod = 21.6 μg g$^{-1}$
ECOSYSTEM DEVELOPMENT

Soil Fertility

Precipitation

Annual Dry-wet cycles

Nutrient leaching

Parent material

Soil texture

Organisms

Time

Jenny 1941

Topography
Soil Nutrient content Forest diversity

• Temperate forests:
  – Old Russian scientists already noticed that soils under broadleaf vs needleleaf forests were different.
  – Led to incorporation of organisms into the soil development function of Jenny (1941)
    • $S = f(\text{parent material, topography, time, climate, organisms, …...})$

• High diversity in tropical forests makes analyses difficult
Per plot 300 soil samples are taken from 0-10cm; 1 per 20x20m block (composite of 3 samples taken at the center, 2 and 8m away from the center).

Used PC analyses for soil nutrients to correlate with plant species with either a minimum of 5 or 50 individuals.

John et al. (2007) Soil chemistry and forest diversity
Niche breaths indicate different nutrients most influential on species distribution.

**Conclusion:** soil nutrient content influences plant diversity.

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**Fig. 3.** The influence of soil nutrients on niche structure in the three forest dynamics plots. The values on the y axis are areas under the cumulative curves of species niche breadth values for each soil variable. The greater the area for a given soil variable, the greater the effect of that variable on niche structure. The values in parentheses are the total number of species analyzed at each site.

**Table 2. Soil nutrient concentrations and pH values in the three forest dynamics plots**

<table>
<thead>
<tr>
<th>Site</th>
<th>Al</th>
<th>B</th>
<th>Ca</th>
<th>Cu</th>
<th>Fe</th>
<th>K</th>
<th>Mg</th>
<th>Mn</th>
<th>N</th>
<th>N_{min}</th>
<th>P</th>
<th>Zn</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCI</td>
<td>1,013.8</td>
<td>0.944</td>
<td>1732.5</td>
<td>8.08</td>
<td>178.5</td>
<td>171.8</td>
<td>298.9</td>
<td>370.7</td>
<td>25.92</td>
<td>17.84</td>
<td>2.90</td>
<td>5.66</td>
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</tr>
<tr>
<td></td>
<td>(233.3)</td>
<td>(0.536)</td>
<td>(743.2)</td>
<td>(2.04)</td>
<td>(46.2)</td>
<td>(74.7)</td>
<td>(128.0)</td>
<td>(155.6)</td>
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<td>(12.82)</td>
<td>(1.62)</td>
<td>(4.14)</td>
<td>(0.34)</td>
</tr>
<tr>
<td>La Planada</td>
<td>3,732.4</td>
<td>—</td>
<td>168.6</td>
<td>2.20</td>
<td>562.2</td>
<td>62.5</td>
<td>26.1</td>
<td>3.9</td>
<td>22.71</td>
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<tr>
<td>Yasuni</td>
<td>1,796.7</td>
<td>—</td>
<td>409.9</td>
<td>1.06</td>
<td>284.1</td>
<td>99.8</td>
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For each plot, the top row gives plot-wide mean values (mg/kg) of 10 \times 10 m quadrats, and the values in parentheses are standard deviations. N_{min}, N mineralization rates (mg/kg per 28 days).
Niche breadths indicate different nutrients most influential on species distribution

**Conclusion:** soil nutrient content influences plant diversity

**Problems:**
- Causality problem, also possible: soil nutrient differences due to plant species composition
- Strongest influence of K and Ca on niche structure at La Planada and Yasuni, respectively is surprising.
- Only 0-10cm of soil sampled. Depth most strongly influenced by vegetation.

![Soil nutrient concentration and pH values in three forest dynamics plots](image)

**Fig. 3.** The influence of soil nutrients on niche structure in the three forest dynamics plots. The values on the y axis are areas under the cumulative curves of species niche breadth values for each soil variable. The greater the area for a given soil variable, the greater the effect of that variable on niche structure. The values in parentheses are the total number of species analyzed at each site.

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Contrary evidence

Plantation La Selva, CR:
- Monoculture or mixed species
- 32x32m plots
- 3 Randomized blocks with 4 replicates and 6 treatments (4 monocultures, mixed, and fallow)

Main conclusions:
- Above-ground biomass and nutrient mass species very different
- Main nutrient differences in stem biomass, i.e., strongly related to GR
- 5 years after planting significant effects on soil P concentration (to 35 cm depth)

Montagnini 2000
Contrary evidence

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- 5 years after planting significant effects on soil P concentration (to 35 cm depth)

If monocultures already influence soil P below them after 5 years, why not large (>300 yr old) trees in diverse forests?
Summary

• Soil nutrient variability in three tropical forest plots appears to influence 36-51% of species distribution

• Multiple nutrients most influential at different sites

• I am not convinced that the John et al. paper really represents soil nutrient influence on tree species distribution
Land-use Fertilization effects

- Forest growth?
- Species effects?
- Nutrient cycling?

Land-use change leads to
- dust N and P fertilization from agriculture
- fire adds NH₃, P, and micronutrients to natural ecosystems
Hawaii as a model of ecosystem development over 4.1 Myrs

Fertilization Experiments on Chronosequence

Tree growth

Treatment: Control   N     P    N+P

Young sites N-limited
Middle sites jointly-limited
Old sites P-limited

Effect of soil nutrient status on Ecosystem response to fertilization

Fig. 12. N cycles in N-limited (left side of figure, gray arrows) and P-limited (right side of figure, black arrows) tropical forests. Only processes and pools related to soil N-oxide emissions in this study are shown. The size of arrows represents the relative rate of each process; the size of boxes represents the relative size of each pool.
**P fertilization**

P fertilization in CR
- Microbial growth in P-poor soils is P limited
- Respiration increases only when both C and P added

**N, P, and M fertilization**

Methods:
- Continuously fertilized forest plots with N, P, and M (mix of micronutrients)
- Measured litter decomposition on litter sampled over a period of 6 yrs

Findings:
- Enhanced reproductive litter on N fertilized plots
- K and P enhance cellulose and litter decomposition

Conclusions:
- Tropical forests subject to multiple nutrient limitation
- N fertilization could change species reproductive investment and potentially long-term competition

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Cleveland et al. (2005)
Fertilization summary

• Limited data suggest that fertilization effects can change
  – Forest carbon and nutrient uptake
  – species competition
  – Litter decomposition rates
  – N cycling

Davidson et al. (2007) paper suggest that this can have strong effects within present day human life-times
Houlton Climate driven switch N uptake

Plant species do not care what source of nitrogen they use!
Figure 3 | Model results for different hypotheses across terrestrial biomes at steady state. a–l, The hypotheses tested are: (1), temperature-dependent $N_2$ fixation and individual-based P acquisition strategy (consistent with our proposed framework); (2), temperature-dependent $N_2$ fixation and global-commons P acquisition strategy; and (3), constant $N_2$ fixation (no temperature effect) and individual-based P acquisition strategy. a–d, NPP by $N_2$ fixers (grey) and non-fixers (black); e–h, the $N_2$ fixation rate; i–l, the nutrient-limitation intensity for $N_2$ fixers (grey) and non-fixers (black). Nutrient-limitation intensity was calculated as the difference in N availability minus P availability, such that positive values indicate P limitation and negative values indicate N limitation.
Because the first gradient is so strongly associated with the abundance of legumes (Fabaceae; Fig. 1f), we investigated the geographical distribution of two characteristics commonly associated with the family: nitrogen-fixing nodulation and ectomycorrhizal associations, both assumed adaptations to low-fertility soils. Ectomycorrhizal association is apparently insignificant in northern South America (Fig. 1e), apart from small areas in Guyana (where the ectomycorrhizal genus Dicyme is common) and the upper Rio Negro (where the ectomycorrhizal genus Aldina is common). Not surprisingly, individuals of nodulating genera are more common on poor soils (Figs 1g and 2e). However, individuals of nodulating genera represent a smaller fraction of all Fabaceae on poor soils than they do on rich soils (Fig. 2f), and nodulation within Fabaceae is strongly influenced by precipitation.
$\delta^{15}$N evidence

Nardoto (2005)
So why do legumes not fix N?

- Too carbon intensive?
- Too P intensive?

But why are they so abundant then?

- Are very important as early colonizers
- Relatively fast growers
- Are more versatile
Soil development summary

- Organisms need both soil and atmosphere derived nutrients
- Under natural conditions soil nutrient changes are relatively fast for atmospheric derived nutrients, but slow for soil derived nutrients
- Time frame of soil derived nutrients depends on soil depth and nutrient retention
Supporting evidence

Table 1. Means ± 95% confidence intervals of soil variables (0–15 cm depth mineral soil) sampled underneath the crowns of four tree species and neighbouring Pentaclethra trees (data for the paired Pentaclethra trees are listed beneath each focal tree species).

<table>
<thead>
<tr>
<th></th>
<th>Ca (cmol(+)/kg⁻¹)</th>
<th>K (cmol(+)/kg⁻¹)</th>
<th>Mg (cmol(+)/kg⁻¹)</th>
<th>P (μg g⁻¹)</th>
<th>%C</th>
<th>%N</th>
<th>pH(CaCl₂)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Albizia</td>
<td>0.04 (0.02)</td>
<td>0.24 (0.03)</td>
<td>0.35 (0.05)</td>
<td>31.11 (7.98)</td>
<td>6.00 (0.79)</td>
<td>0.46 (0.05)</td>
<td>3.52 (0.18)</td>
</tr>
<tr>
<td>Pentaclethra</td>
<td>0.06 (0.05)</td>
<td>0.21 (0.03)</td>
<td>0.30 (0.04)</td>
<td>20.67 (4.38)</td>
<td>5.13 (1.07)</td>
<td>0.40 (0.07)</td>
<td>3.59 (0.17)</td>
</tr>
<tr>
<td>Dipterix</td>
<td>0.13 (0.06)</td>
<td>0.26 (0.04)</td>
<td>0.46 (0.12)</td>
<td>28.51 (11.59)</td>
<td>5.72 (0.68)</td>
<td>0.45 (0.04)</td>
<td>3.66 (0.16)</td>
</tr>
<tr>
<td>Pentaclethra</td>
<td>0.08 (0.04)</td>
<td>0.51 (0.66)</td>
<td>0.42 (0.28)</td>
<td>26.06 (12.14)</td>
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<td>Hyeronima</td>
<td>0.16 (0.10)</td>
<td>0.35 (0.14)</td>
<td>0.43 (0.15)</td>
<td>52.31 (48.54)</td>
<td>5.55 (1.15)</td>
<td>0.46 (0.09)</td>
<td>3.74 (0.20)</td>
</tr>
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<td>Pentaclethra</td>
<td>0.14 (0.23)</td>
<td>0.29 (0.08)</td>
<td>0.55 (0.40)</td>
<td>49.88 (31.15)</td>
<td>5.05 (0.87)</td>
<td>0.43 (0.09)</td>
<td>3.80 (0.26)</td>
</tr>
<tr>
<td>Lecythid</td>
<td>0.13 (0.07)</td>
<td>0.25 (0.03)</td>
<td>0.35 (0.10)</td>
<td>21.18 (6.17)</td>
<td>4.94 (0.48)</td>
<td>0.39 (0.03)</td>
<td>3.63 (0.20)</td>
</tr>
<tr>
<td>Pentaclethra</td>
<td>0.05 (0.04)</td>
<td>0.24 (0.08)</td>
<td>0.28 (0.13)</td>
<td>23.29 (6.96)</td>
<td>4.78 (0.58)</td>
<td>0.38 (0.04)</td>
<td>3.60 (0.23)</td>
</tr>
</tbody>
</table>

P and K suggest soil variability, though large uncertainty

La Selva, CR:
- 8 trees per species
- 8 samples combined per tree
- Pair wise comparison to avoid soil specific variability

Powers et al. 2005

Results from the DECORANA and cluster analyses (Figs. 7 and 8) suggest that factors related to soil development, such as site fertility, are important in determining the abundance and coverage of dominant species at different sites. The strong relationship be-

Crews et al. 1995

![Fig. 8. Unweighted pair-group cluster analysis of quantitative species composition of chronosequence sites. Percentage values refer to similarities among sites based on percentage similarity coefficient (Kovach 1990).]