The Abdus Salam International Centre for Theoretical Physics

United Nations Educational, Scientific and Cultural Organization

International Atomic Energy Agency

World Year of PHYSICS 2005

SMR 1655 - 15

WORKSHOP ON QUANTITATIVE ECOLOGY
9 to 20 May 2005

Seed size, tree abundances, and habitat preferences in neotropical rainforests: Seed size and species distributions

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Seed size, tree abundances, and habitat preferences in neotropical rainforests:

Seed size and species distributions

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Abdus Salam International Center for Theoretical Physics -- May 2005

Long-standing ecological questions:

Why do species live where they do?

Long-standing ecological questions:

How do species coexist?



Long-standing ecological questions:

Do ecologically important traits influence the distribution and abundance of species?




Alternative approaches to testing "neutrality":

1) Assume that species are ecologically equivalent, and then ask whether their distributions and relative abundances are consistent with this assumption.

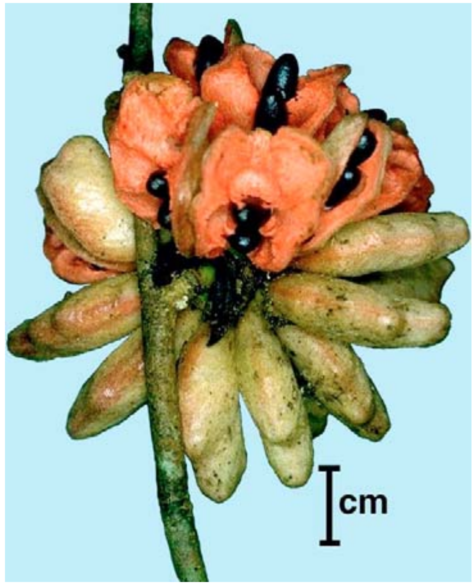
2) Do species' characters whose function we understand violate neutrality?

   That is, do these characteristics predict species distributions and relative abundances?

Comparative analysis of functional traits among 3500 species in 9 neotropical rainforests: an NCEAS working group

Annona muricata

Anacardium occidentale



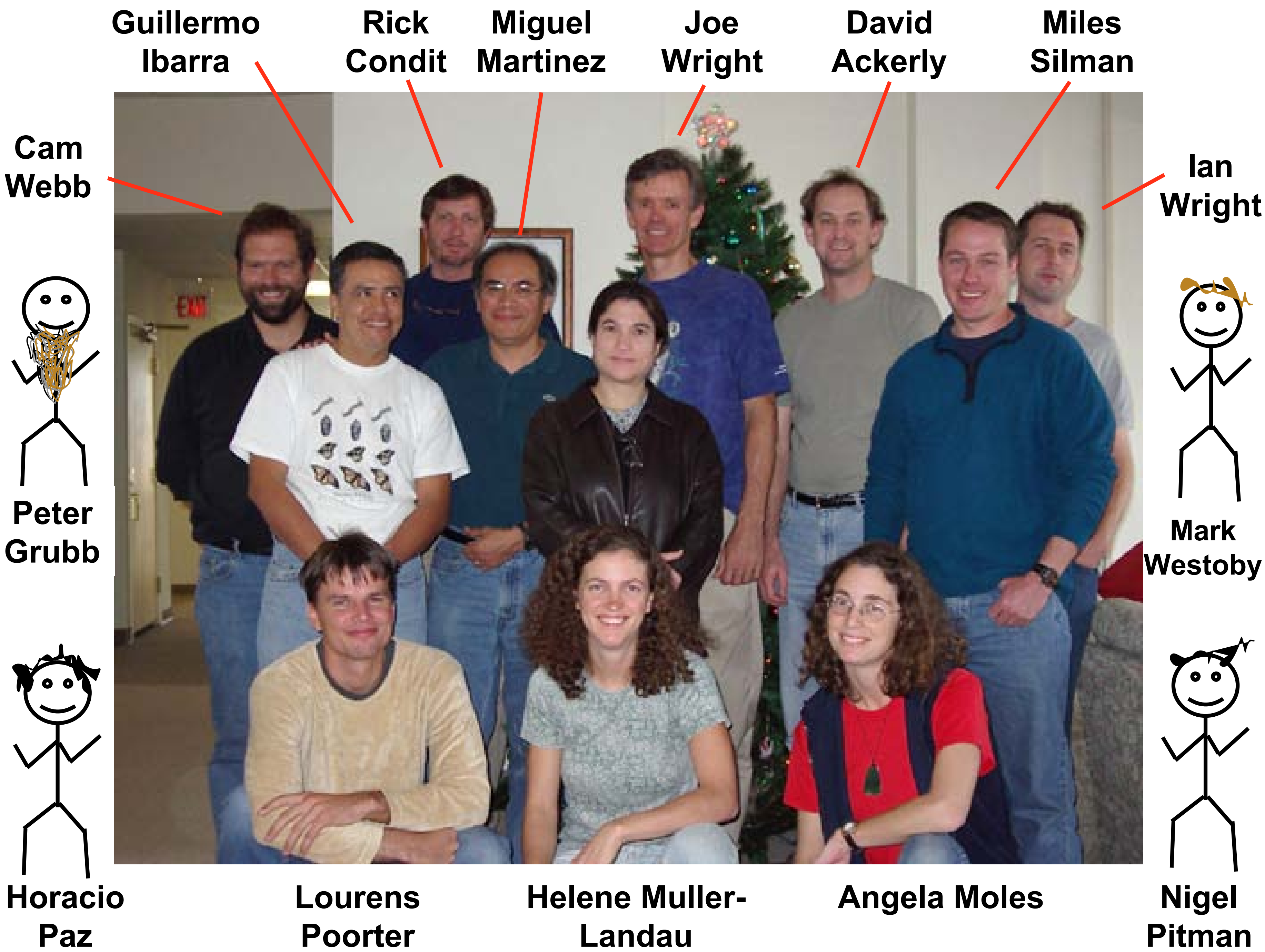
Xylopia cuspidata

Cojoba graciliflora

Bixa orellana

Theobroma cacao

Hamelia patens


Guillermo Ibarra
Rick Condit
Miguel Martinez
Joe Wright
David Ackerly
Miles Silman
Cam Webb
Ian Wright
Peter Grubb
Mark Westoby
Horacio Paz
Lourens Poorter
Helene Muller-Landau
Angela Moles
Nigel Pitman

Seed Size Variation in the Fabaceae in a 3000-hectare reserve

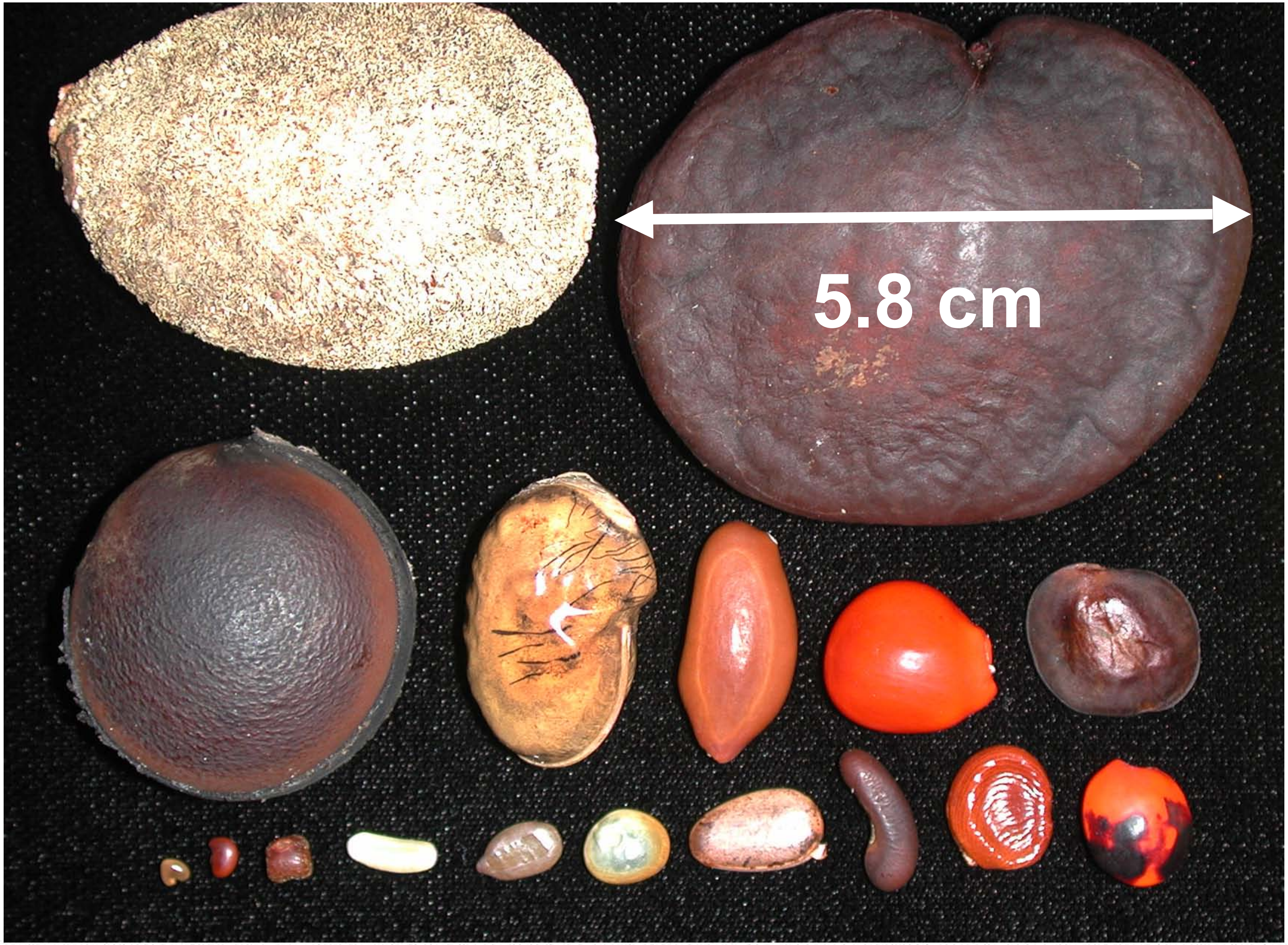
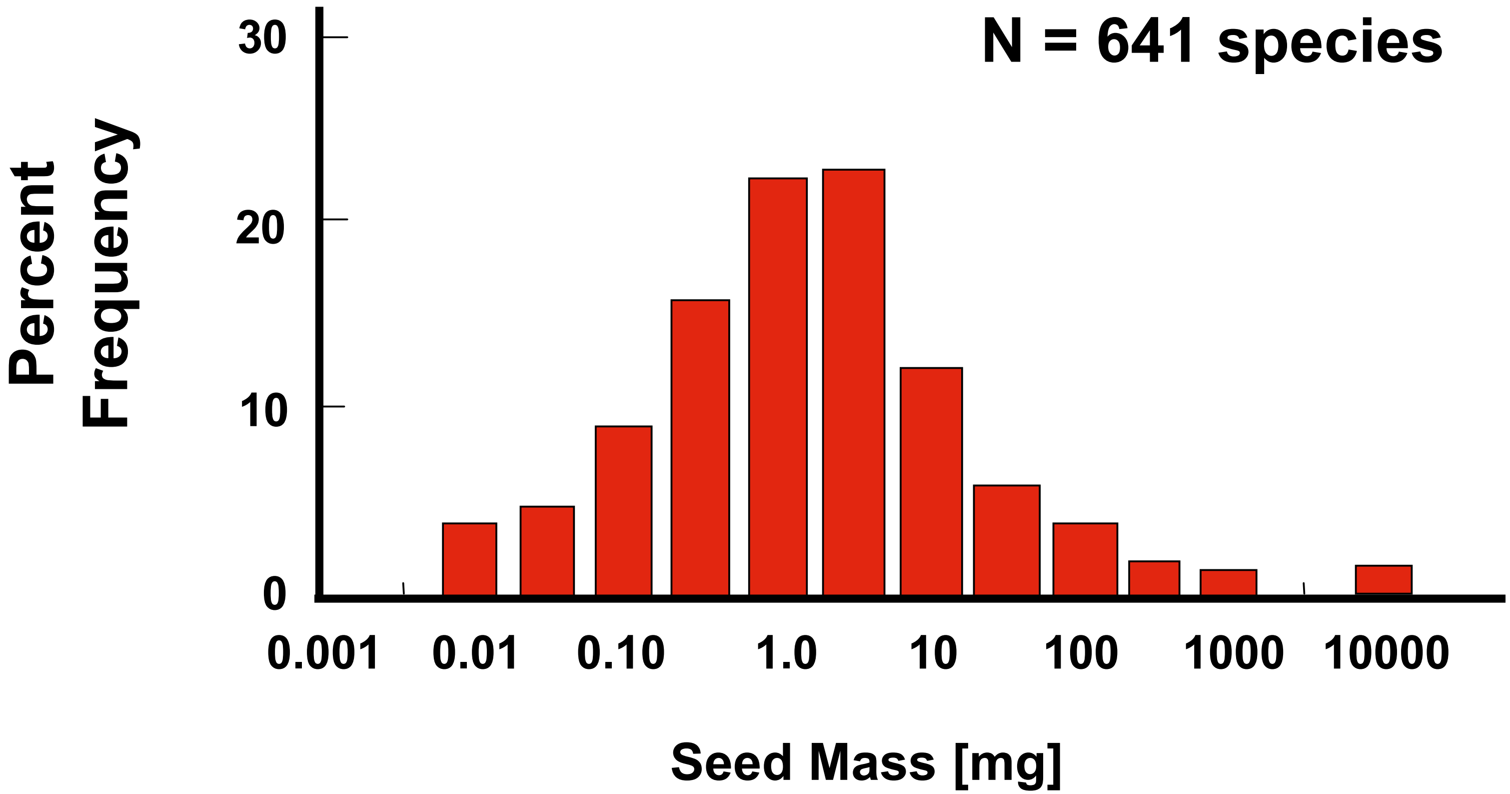


Fig. 1. Seeds of 17 tree species, all from the family Fabaceae, that cooccur in the Peruvian Amazon. The largest seed pictured is 5.8 cm across. The seeds photographed here are a small sample of the 1,200 species of Peruvian Amazonian rainforest seeds in the collection of Susan J. Mazer (Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara) and represent a tiny fraction of the diversity of seed sizes and types represented among the thousands of Amazonian tree species. **Mazer seed collection, photo by Muller-Landau, PNAS. 2003**

Seed size varies over 6 orders of magnitude among species of the Indiana Dunes.



Seed mass ranges from 0.003 mg to > 3100 mg.

Mazer, 1989. *Ecological Monographs* 59

Seed Mass Variation: Indiana Dunes vs. 4 Temperate Floras

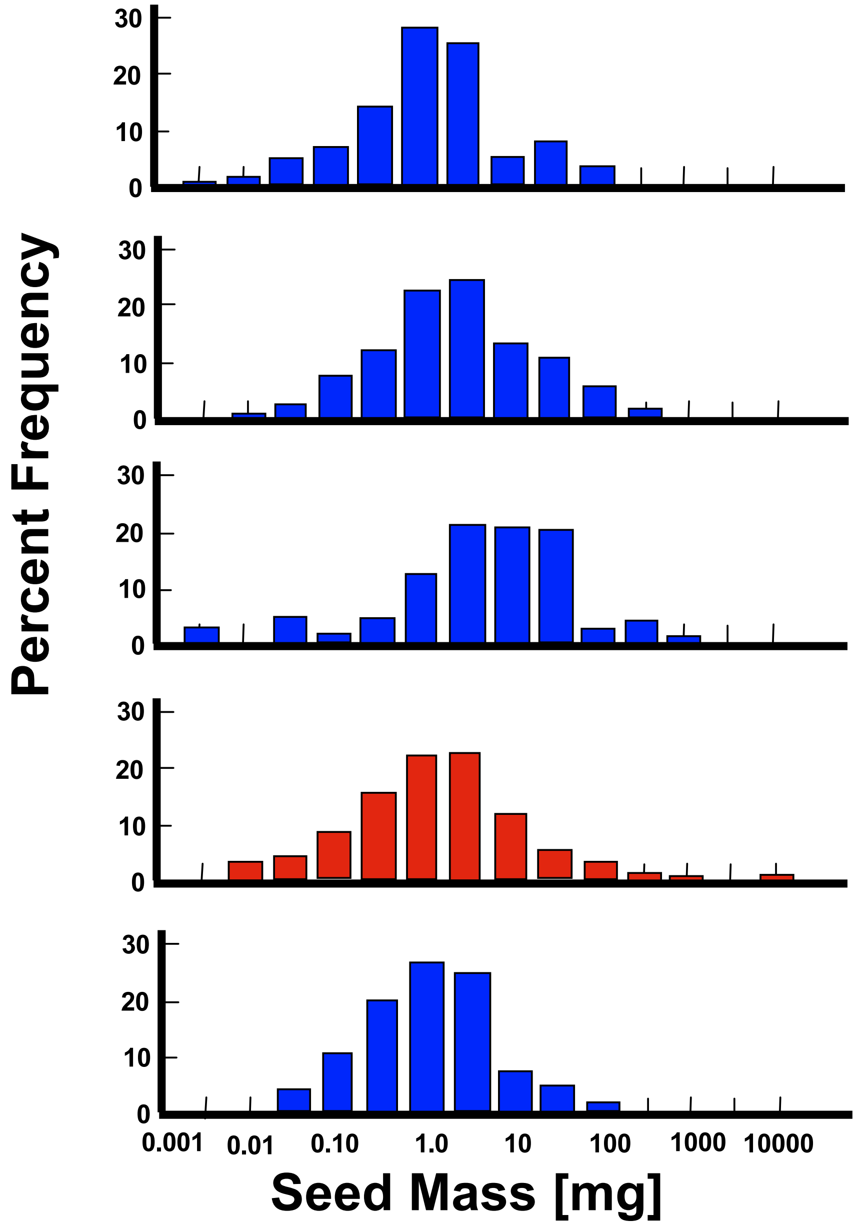
western New South Wales (n = 248)

Central Australia (n = 196)

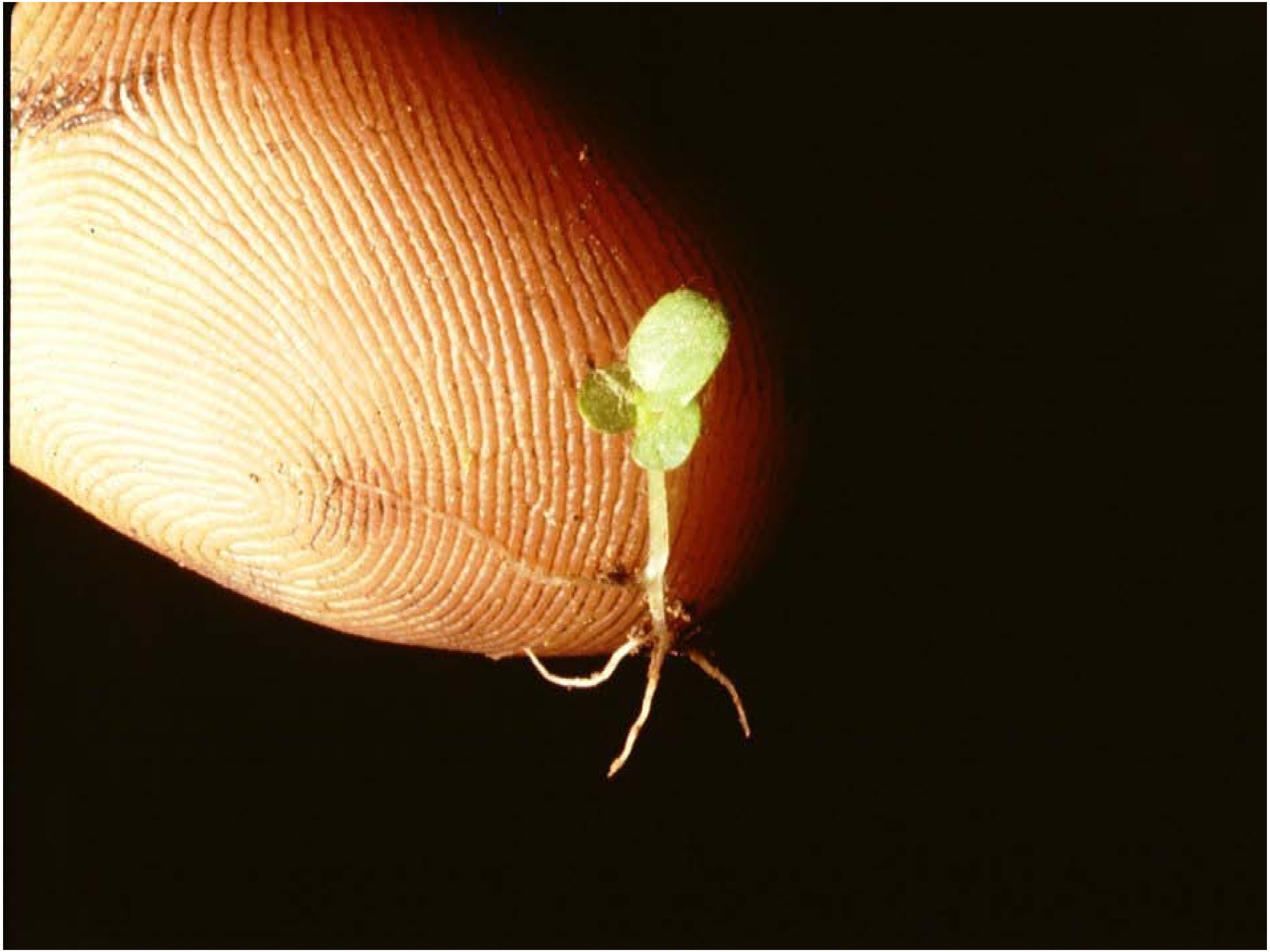
Sydney (n = 308)

Indiana Dunes (n = 641)

Sheffield (n = 266)

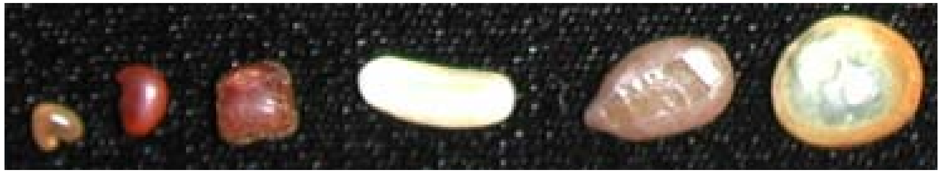


Leishman, Westoby & Jurado, 1995



Does Seed Size Matter?

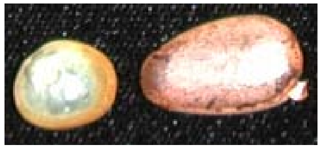
Known Benefits & Costs



Large Seeds	Small Seeds
Emerge even when buried	Can’t emerge from under thick litter layer
Tolerate embryo damage and microbial infection	Vulnerable to damage
Produce seedlings that are tolerant of herbivory or defoliation	Produce smaller seedlings
Provide reserves that help seedlings to persist under low light	Provide few reserves

Does Seed Size Matter?

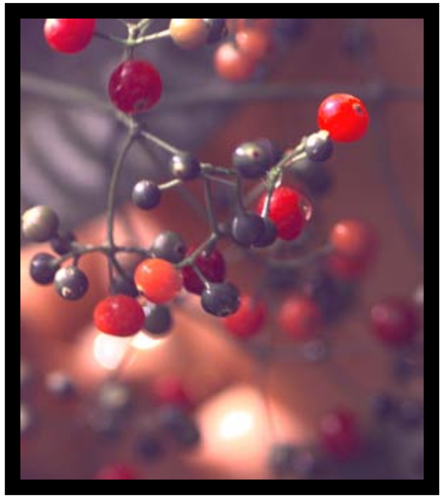
Known Benefits & Costs



Large-seeded Species	Small-seeded Species
Lower fecundity	Higher fecundity/repr. episode
Potentially limited dispersal	Greater array of dispersers
Lower Relative Growth Rates	Higher Relative Growth Rates

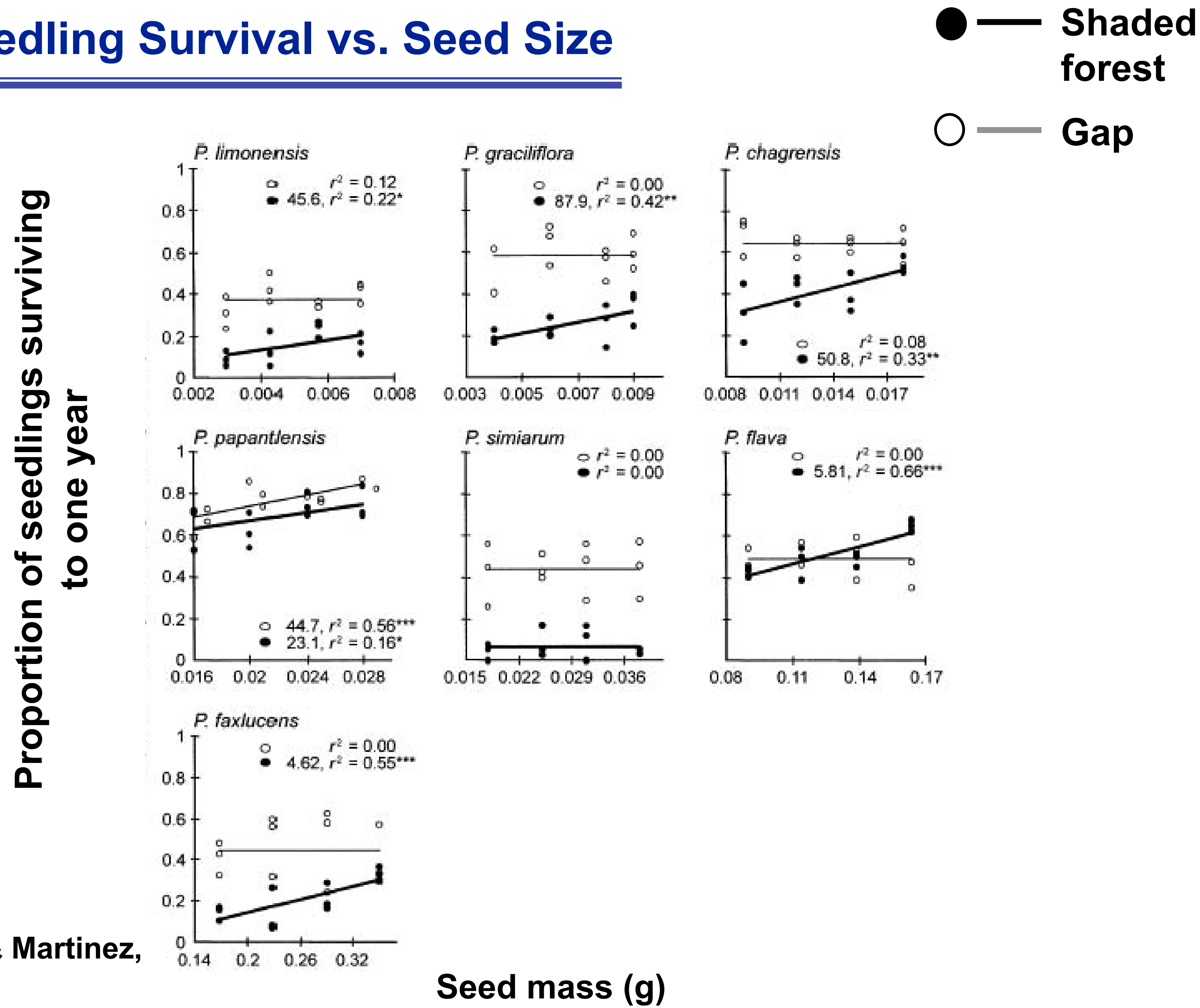
Effects of seed size on performance:
Examples in the genus *Psychotria*






Paz, Mazer & Martinez-Ramos. 1999. Seed mass, seedling emergence, and environmental factors in seven rain forest *Psychotria* (Rubiaceae). Ecology 80

Seedling Survival vs. Seed Size

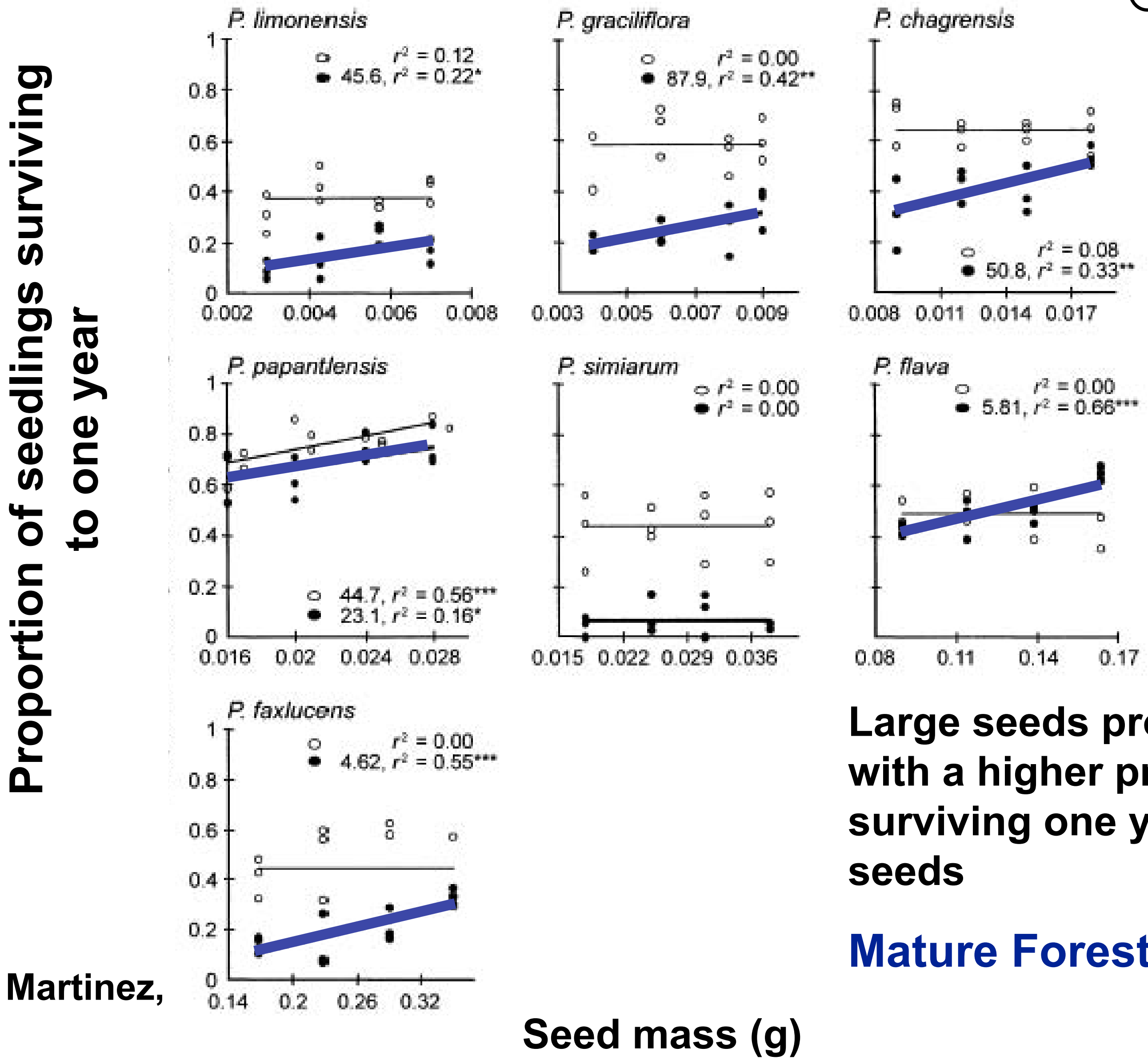


Paz & Martinez, 2003

Seedling Survival vs. Seed Size

● — Shaded forest

○ — Gap



Large seeds produce seedlings with a higher probability of surviving one year than small seeds

Mature Forest: 6 of 7 species

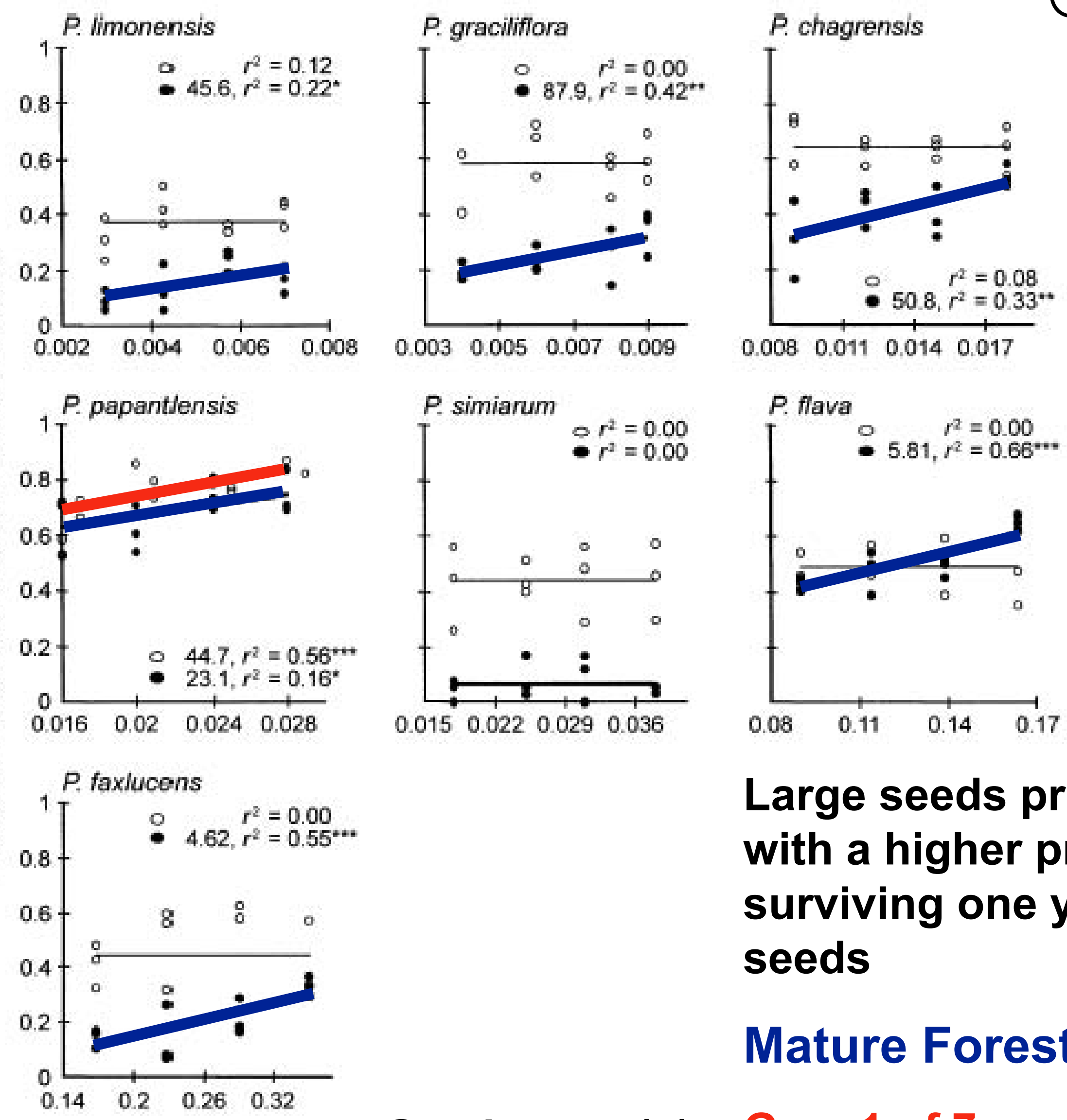
Paz & Martinez, 2003

Seedling Survival vs. Seed Size

● —— Shaded forest

○ —— Gap

Proportion of seedlings surviving to one year



Seed mass (g)

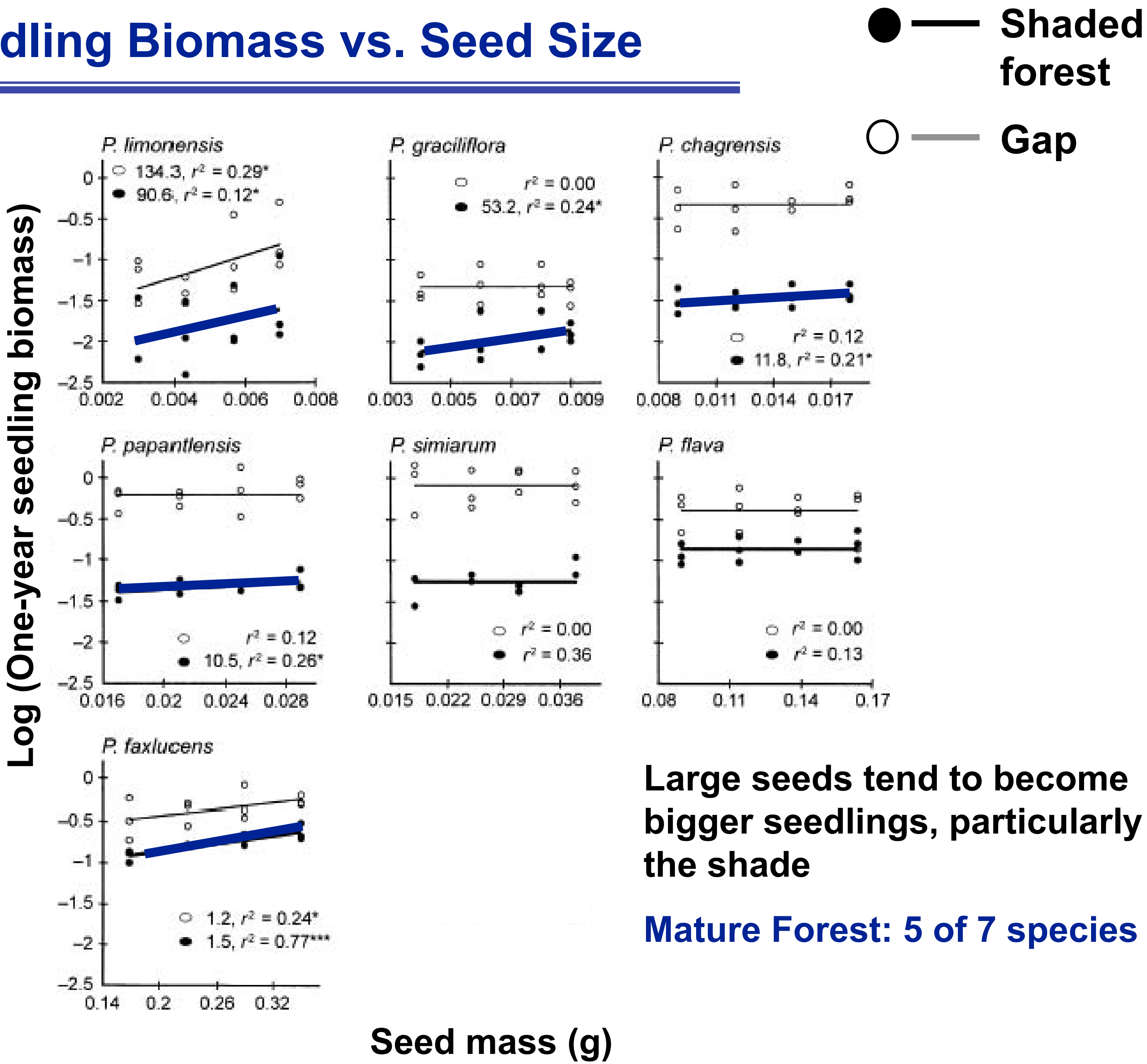
Paz & Martinez, 2003

Large seeds produce seedlings with a higher probability of surviving one year than small seeds

Mature Forest: 6 of 7 species

Gap: 1 of 7 species

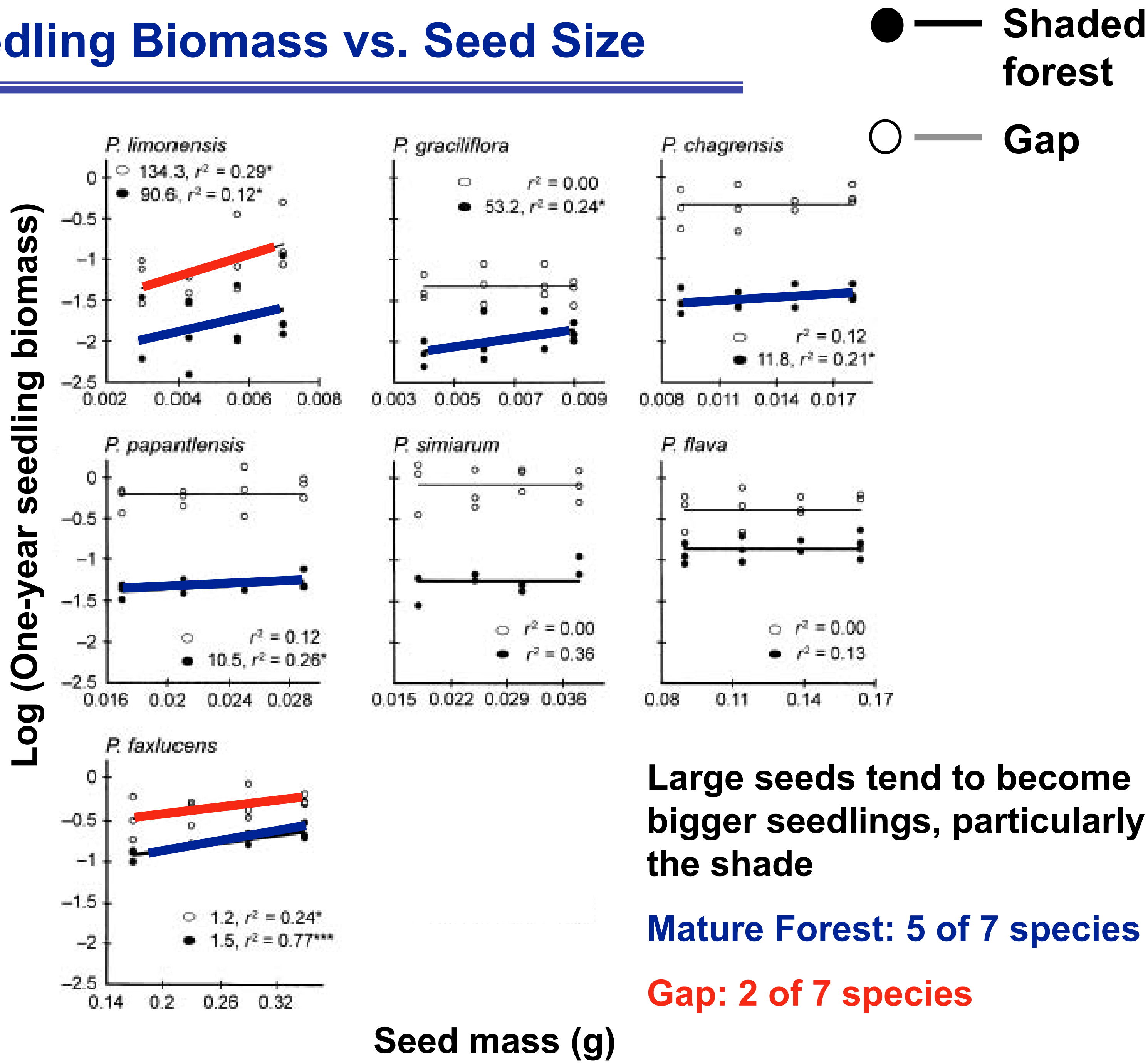
Seedling Biomass vs. Seed Size



Large seeds tend to become bigger seedlings, particularly in the shade

Mature Forest: 5 of 7 species

Seedling Biomass vs. Seed Size



Large seeds tend to become bigger seedlings, particularly in the shade

Mature Forest: 5 of 7 species

Gap: 2 of 7 species

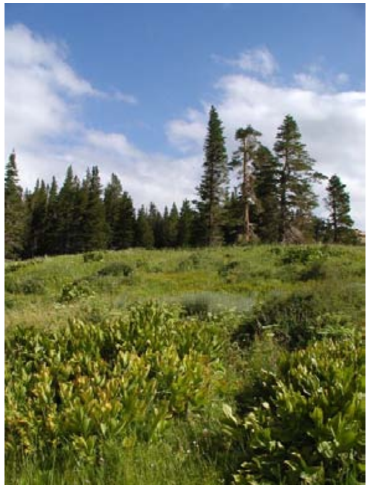
Does seed size matter?

If:

- Seed size affects seedling performance.
- The relationship between seed size and performance differs among habitats.

Then:

- The optimal seed size will differ among habitats.



Does seed size matter?

If:

- Seed size affects seedling performance.
- The relationship between seed size and performance differs among habitats.

Then:

- The optimal seed size will differ among habitats.
- Seed size and adult abundances will be related within habitats.

The Catch:

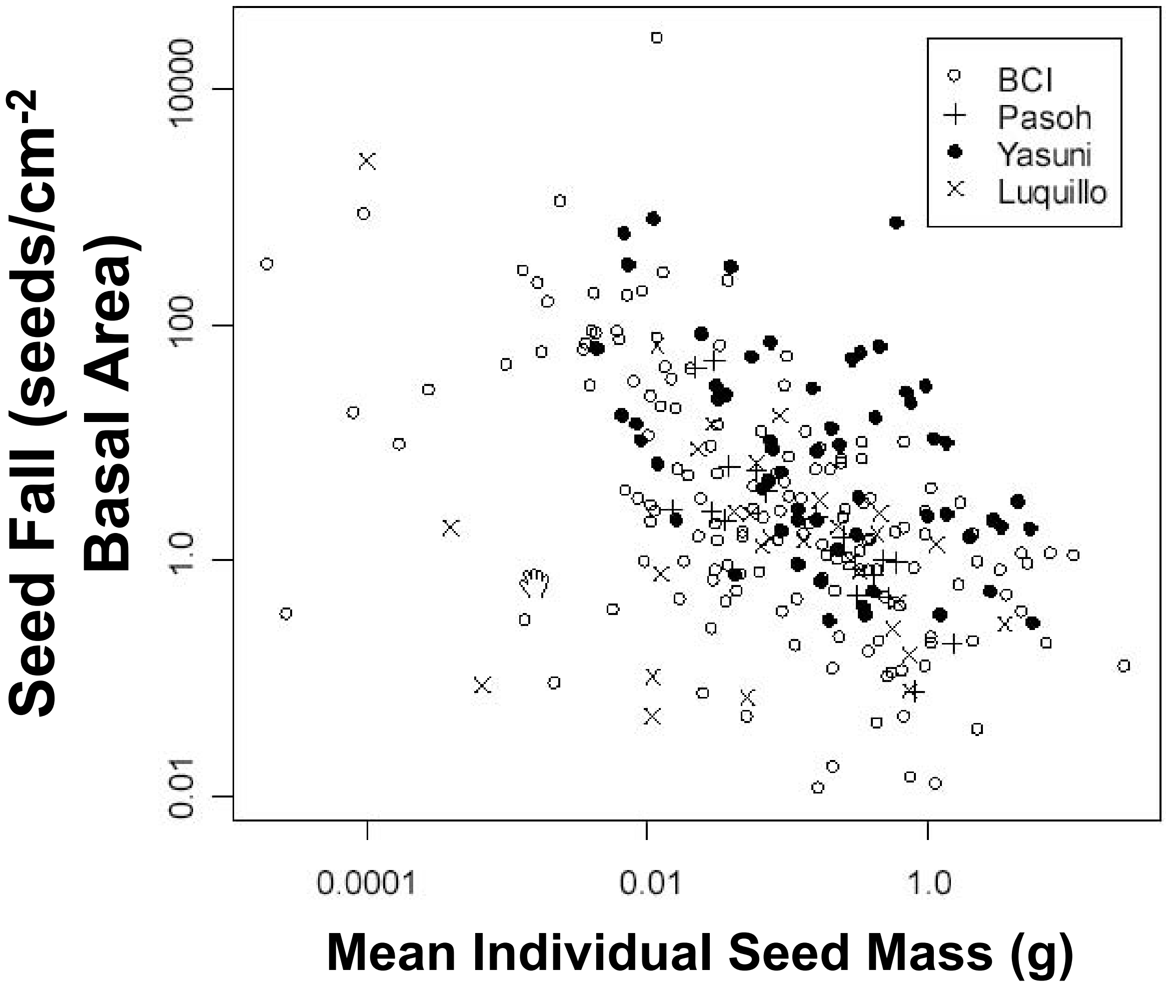
If:

- **There's a strong trade-off between seed size and fecundity….**

Then:

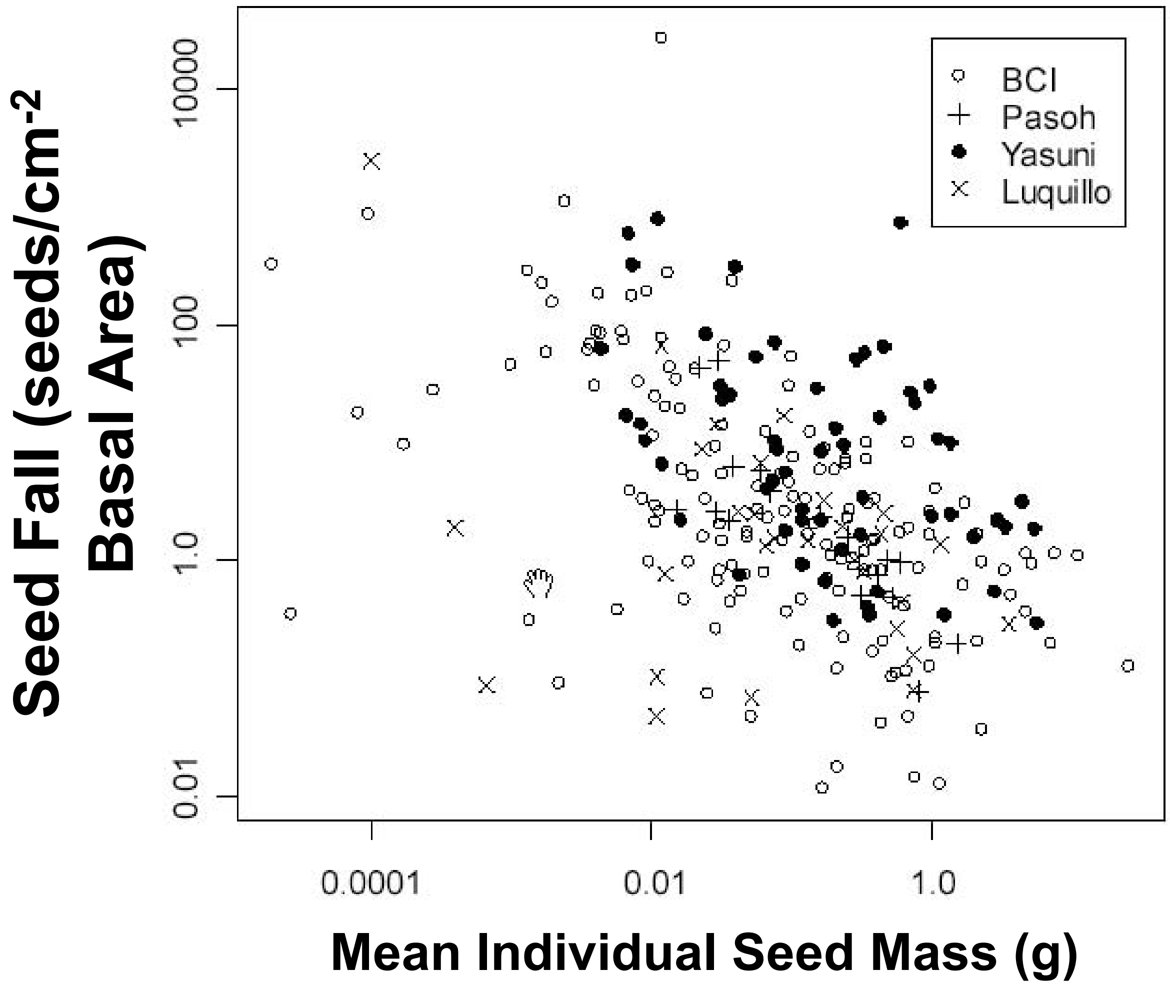
- **The effects of seed size on *seedling* performance will not necessarily translate into an effect of seed size on *adult* abundances.**
- **Seed size might *not* predict adult abundances.**

Trade-off between seed production and seed mass among species in four rainforests



Muller-Landau, Wright, Zimmerman, Chen, Fang Sun, Condit, Foster, Hubbell, Mazer, Noor, Silman, Thompson, LaFrankie, Valencia, & Villa, submitted. CTFS.

Trade-off between seed production and seed mass among species in four rainforests



Large-seeded taxa produce fewer seeds/cm^{-2} of basal area

Detecting the *Ecological* function of seed size

- Does seed size affect seedling performance within species? ✓
- Does seed size predict the abundances of adult trees within habitats?
- Do species sort themselves among habitats by seed size?
- Does seed size predict habitat preferences?

Detecting the *Evolutionary* significance of seed size

- **Within habitats: is evolutionary divergence in seed size associated with differences in abundance?**

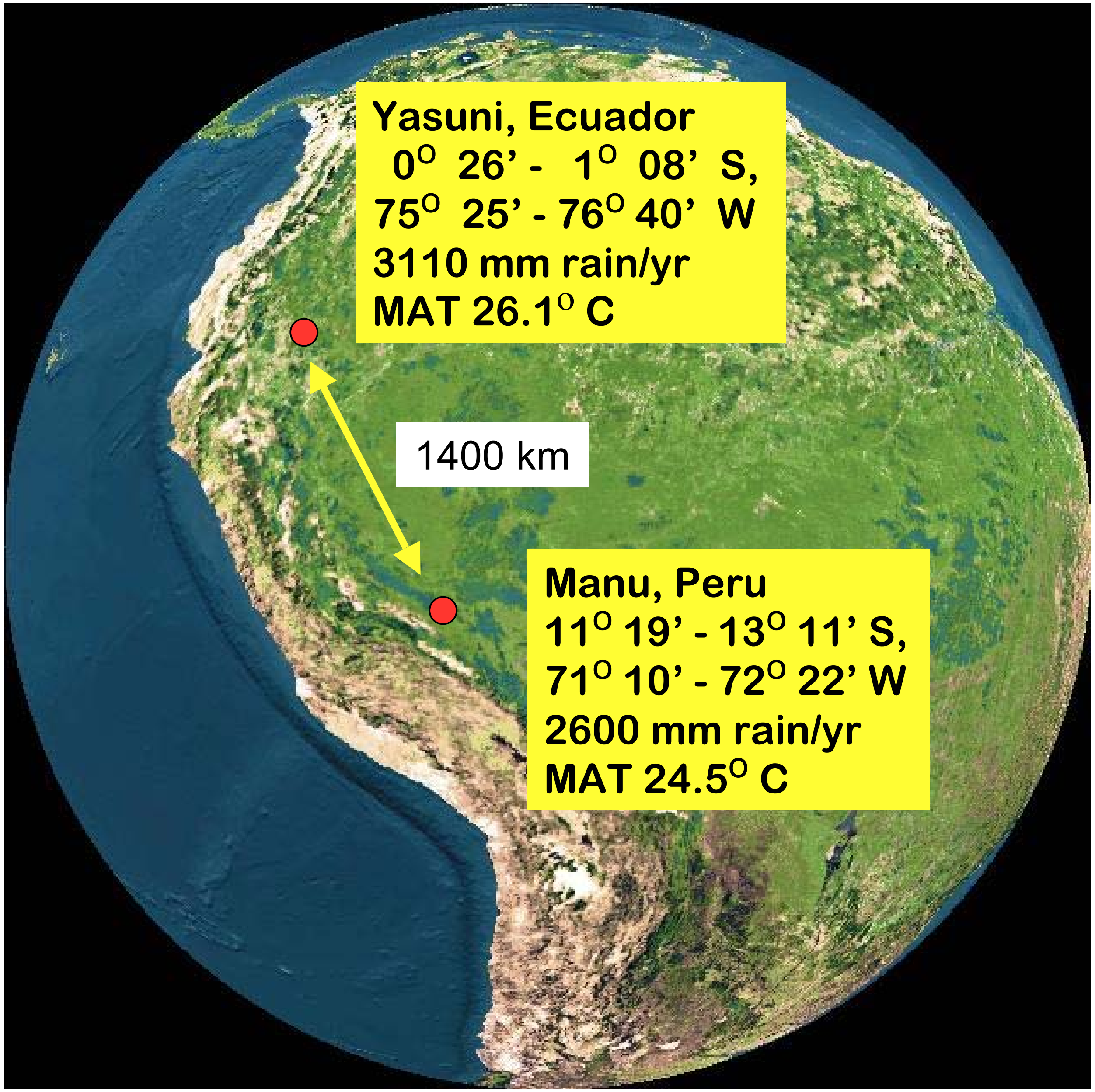
- **Between habitats: Is evolutionary divergence in seed size associated with differences in habitat preference?**

Compare extant patterns of tree distributions and abundances with inferred patterns of seed size evolution.

Seed size, abundance, and adaptation in neotropical rainforests:

ecological and evolutionary perspectives

http://www.fourmilab.ch/cgi-bin/uncgi/Earth



The two sites share > 240 species (out of ~1200)

Sandier soils, less organic matter, higher N, lower Mg

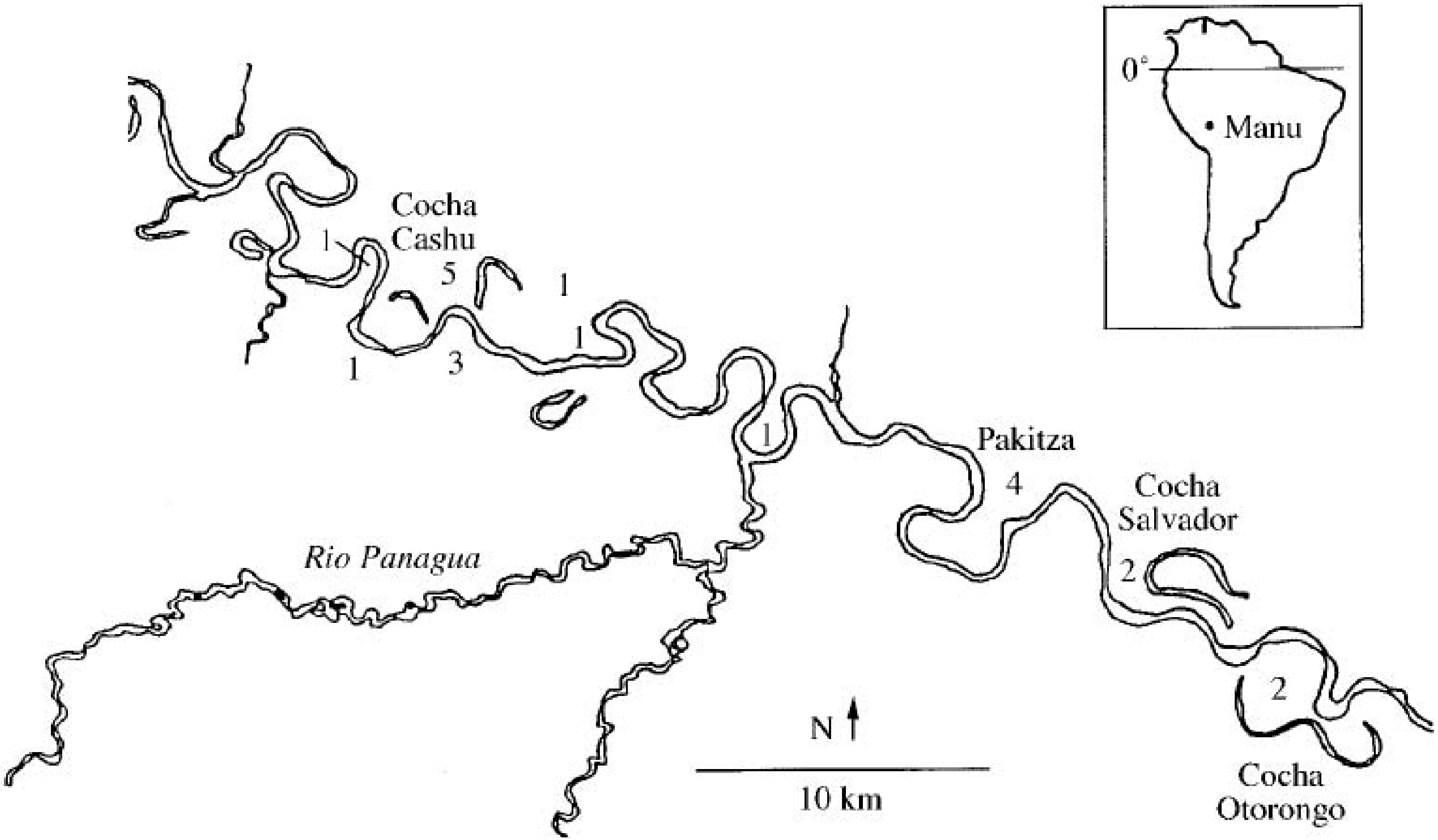
http://www.fourmilab.ch/cgi-bin/uncgi/Earth


QUITO
Bahia de Caráquez
Manta
Portoviejo
Chone
Quevedo
Machachi
Latacunga
Ambato
Baeza
Tena
Puyo
Guaranda
Riobamba
PARQUE NACIONAL MACHALILLA
Babahoyo
GUAYAQUIL
Milagro
Naranjal
ECUADOR
Azogues
Cuenca
Machala
Tumbes
Zorritos
Santa Rosa
Loja
Zamora
Macará
PARQUE NACIONAL PODOCARPUS
Lobitos
Punta Pariñas
Sullana
Paita
Chulucanas
La Unión
Castilla
Bayovar
Punta Negra
Jayanca
Olmos
Chiclayo
Jaén
Chirinos
Moyobamba
Chachapoyas
Tarapoto
Chazuta
Bellavista
Juanjuí
Huicungo
Cajamarca
Chepén
Puerto Chicama
Trujillo
Chocope
Virú
Chimbote
Casma
Nevado Huascarán 6746 m
PARQUE NACIONAL HUASCARÁN
Huánuco
Tingo María
Puerto Inca
Pucallpa
Masisea
Nevado Yerupaja 6634 m
Barranca
Huacho
Huaral
LIMA
Chosica
La Oroya
Cerro de Pasco
Junín
Tarma
La Merced
Satipo
Atalaya
Huancayo
Huancavelica
Ayacucho
Chilca
Mala
Chincha Alta
Pisco
Ica
Nasca
Palpa
Puquio
San Nicolás
Camaná
Ocoña
Atico
Arequipa
Moquegua
Ilo
Tacna
Tarata
Cusco
Quillabamba
Machupicchu
Abancay
Sicuani
Juliaca
Puno
LA PAZ
Nevado Coropuna 6305 m
Nevado Chachani 6075 m
PARQUE NACIONAL DEL MANU
Iñapari
Puerto Maldonado
Quince Mil
Alto Purús
Urubamba
Ucayali
Yurimaguas
Iquitos
Tamshiyacu
San Joaquin de Omaguas
Requena
Concordia
Intutu
Andoas
Barranca
Jeberos
Lagunas
PERU
Orellana
Contamana
Pebas
Puerto Leguízamo
Puerto Tolosa
Araracuara
La Pedrera
El Encanto
Arica
Santa Clotilde
COLOMBIA
Santa Clara
Tarapacá
Leticia
Benjamin Constant
Caballococha
Esperança
Jutaí
BRAZIL
AMAZONAS
Eirunepé
Envira
ACRE
Tarauacá
Feijó
Cruzeiro do Sul
Porto Valter
Foz do Jordão
Puerto Portillo
Taumaturgo
Nuevo Rocafuerte
PARQUE NACIONAL YASUNÍ
Tarqui
Napo
kilometer
0
100
200
300

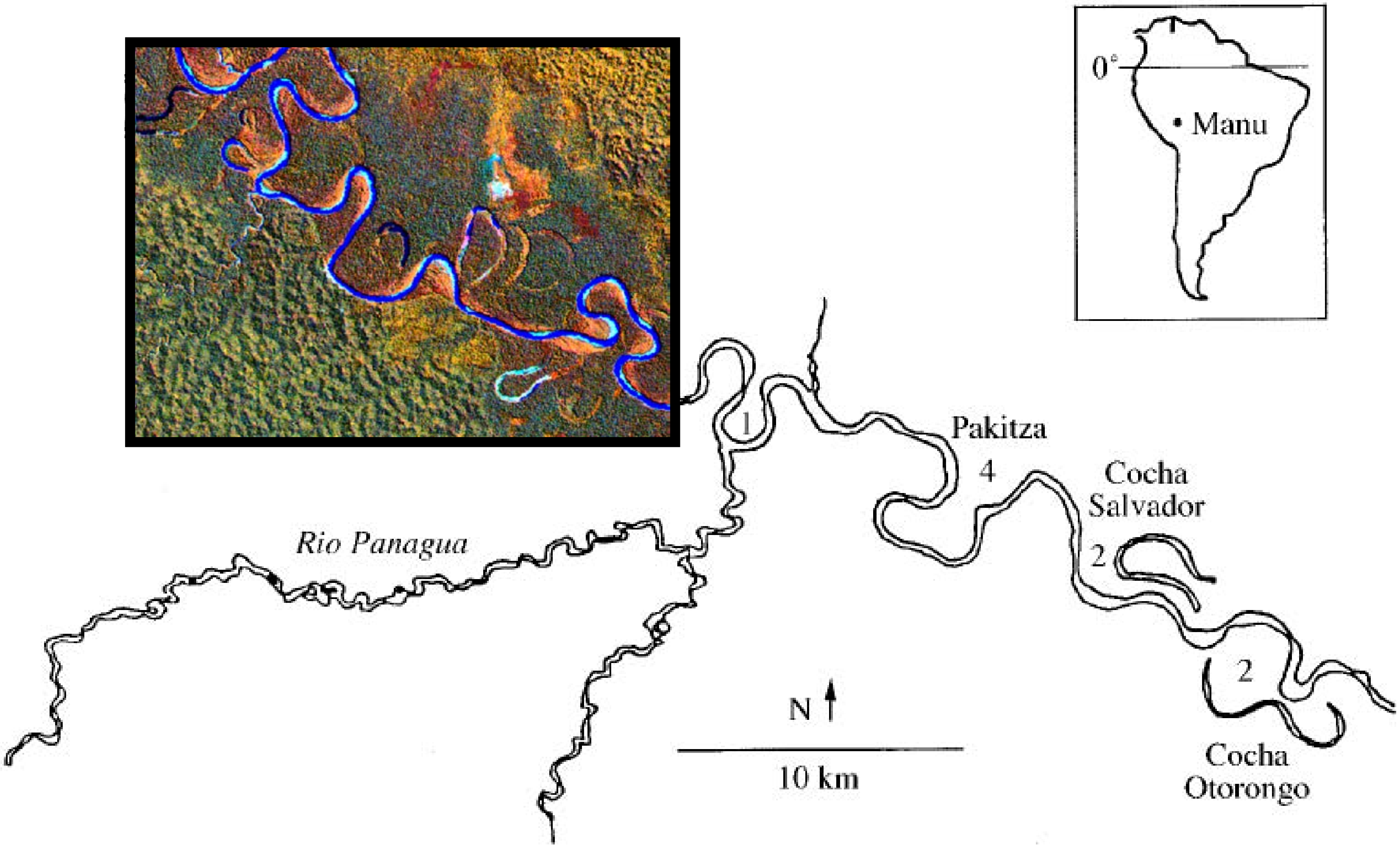
TREE SPECIES DISTRIBUTIONS IN AN UPPER AMAZONIAN FOREST

NIGEL C. A. PITMAN, JOHN TERBORGH, MILES R. SILMAN, AND PERCY NUNEZ V.

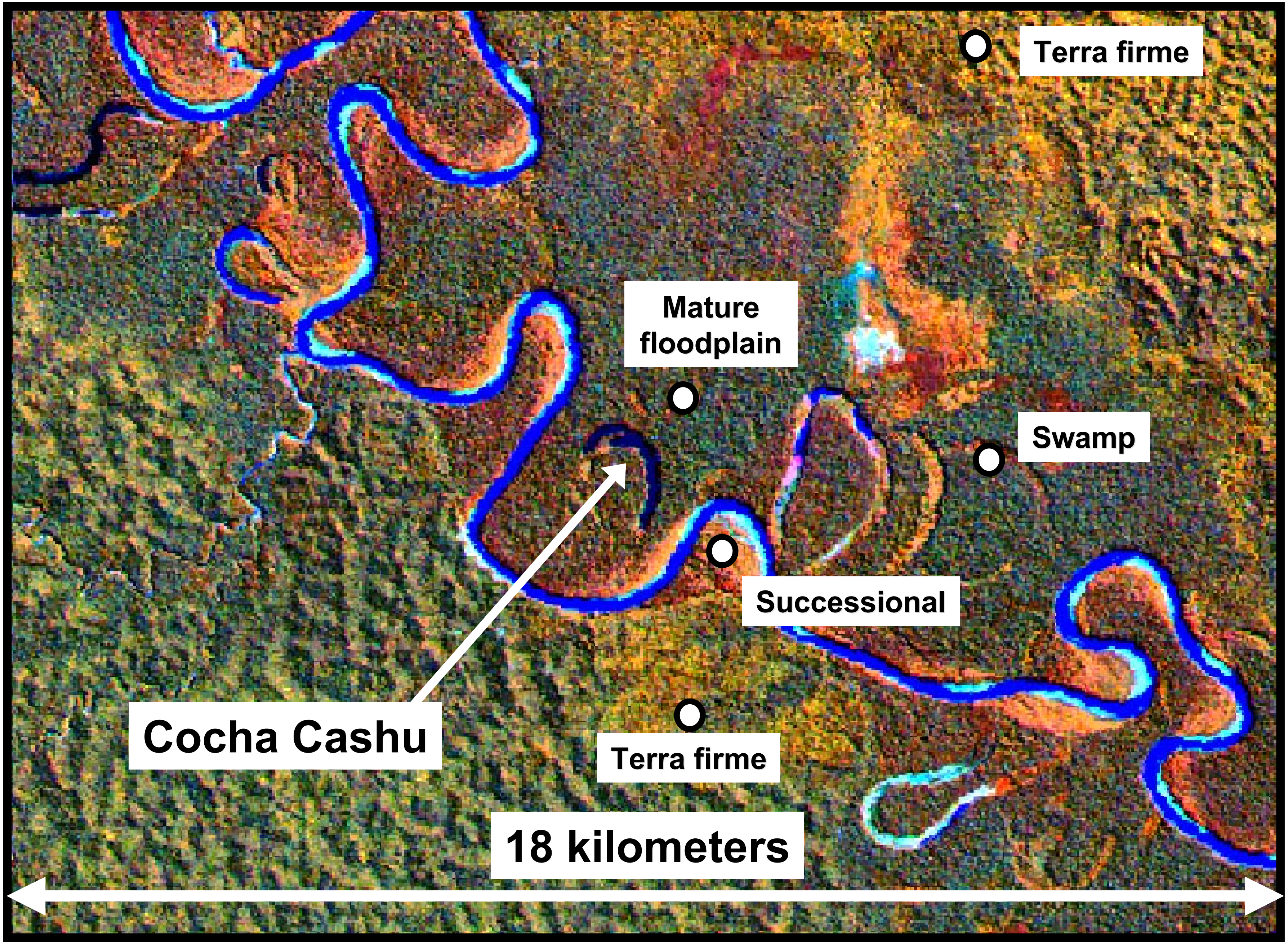
Ecology, 80(8), 1999, pp. 2651–2661

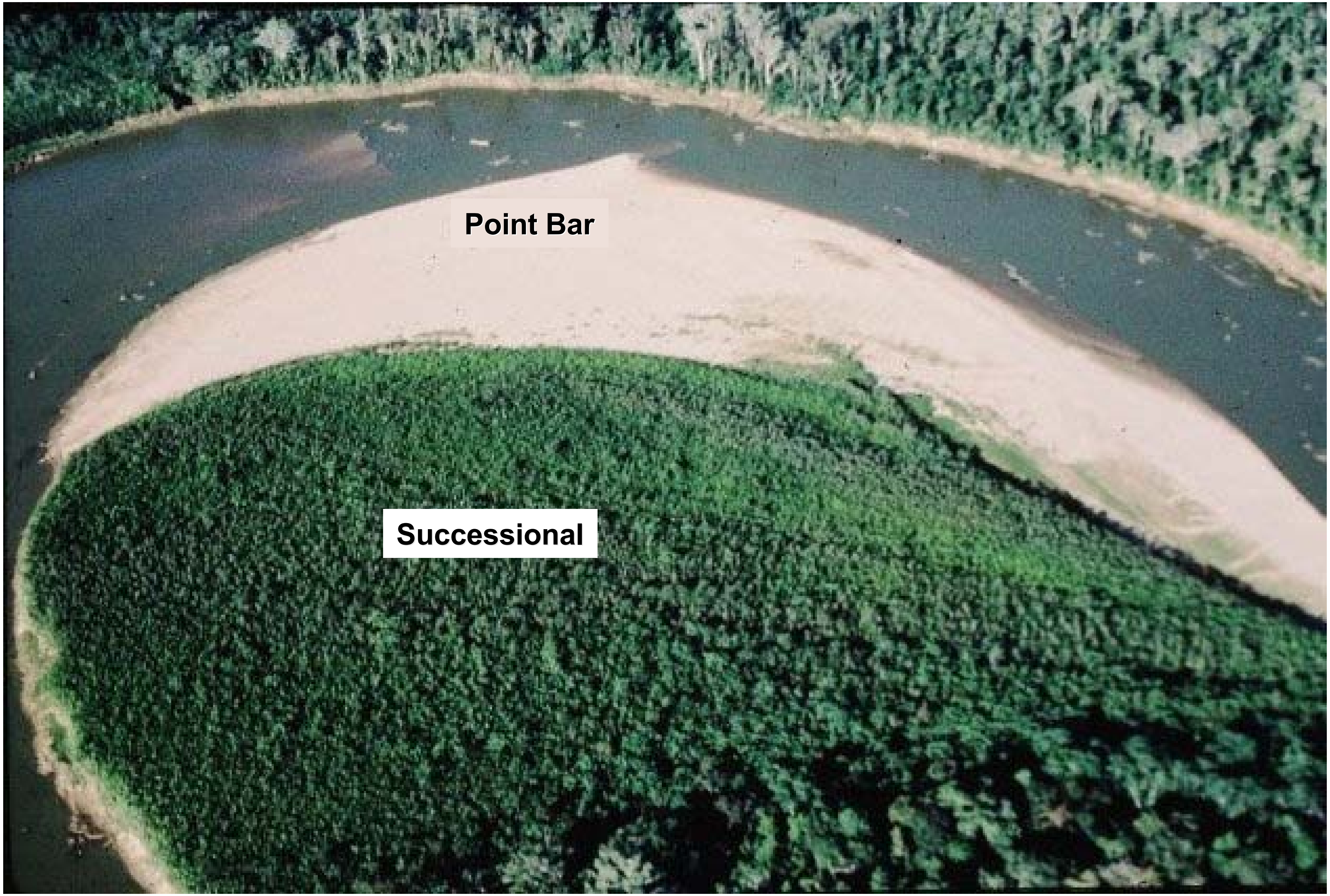


A stretch of the Manu River in the vicinity of the Cocha Cashu Biological Station, Madre de Dios, Peru. The locations of observed 1-2-hectare plots are given by numbers, which also indicate how many plots were sampled at each site.



0°
Manu
Pakitza
4
1
Cocha
Salvador
2
2
Cocha
Otorongo
Rio Panagua
N
10 km


Terra firme
Mature floodplain
Swamp
Successional
Cocha Cashu
Terra firme
18 kilometers


Point Bar
Successional


Mature
floodplain
Successional

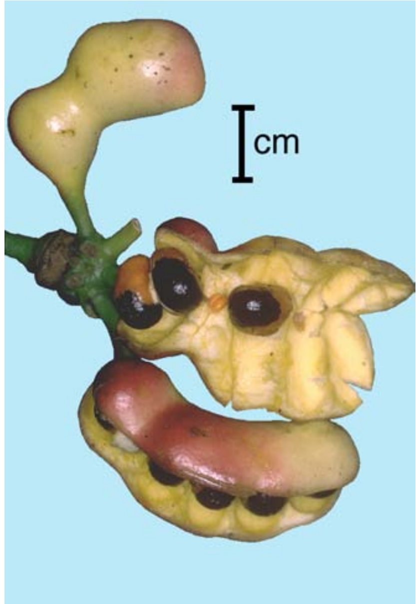

Terra firme

Photo credit: Valerie McKenzie

Regions, habitats, and species diversity

Region	Habitat	# Plots	Total Area Surveyed (ha)	Total # Species (trees& shrubs > 10 cm)	# Species with known seed volumes
Manu	Successional	5	10.5	178	102
Manu	Floodplain	9	16.26	609	267
Manu	Terra Firme	26	27	948	327
Manu	Swamp	5	5.5	234 Σ Occur. = 1969 Σ # Spp = 1127	113 Σ Occur. = 809 Σ # Spp = 363
Yasuni	Floodplain	6	6	565	175
Yasuni	Terra Firme	15	15	1011	257
Yasuni	Swamp	4	5	245 Σ Occur. =1821 Σ # Spp = 1196	78 Σ Occur. = 510 Σ # Spp = 290

Astronium lecontei



Cymbopetalum brasiliens

Mendoncia gigas

Mendoncia glabra

Mendoncia hirsuta

Mendoncia sprucei

Poupartia amazonica

Tapirira guianensis

Mazer & Cornejo. In prep. Photographic field guide to the fruits and seeds of 1000 species of the Tambopata Wildlife Reserve, southeastern Peru

Sources of Data

Seed Identification & Sizes:

Susan Mazer & Fernando Cornejo
Miles Silman & Nigel Pitman

Tree Identification & Abundances:

Robin Foster (Field Museum)
Alwyn Gentry (Missouri Botanical Garden)
Miles Silman (Wake Forest University)
Nigel Pitman (Duke University)
John Terborgh (Duke University)
Elizabeth Losos (Smithsonian)
Percy Nunez (Peru) & colleagues

Most common species of Successional Zone

Includes species without seed size

	Manu	Trees/ ha
Euphorbiaceae	*Sapium glandulosum*	38.10
Meliaceae	*Guarea guidonia*	36.57
Flacourtiaceae	*Casearia decandra*	21.14
Moraceae	*Ficus insipida*	17.81
Meliaceae	*Cedrela odorata*	16.10
Arecaceae	*Iriartea deltoidea*	13.24
Fabaceae	*Inga ruiziana*	11.71
Fabaceae	*Inga marginata*	10.95
Annonaceae	*Guatteria acutissima*	9.52
Annonaceae	*Rollinia fosteri*	9.24
Moraceae	*Clarisia biflora*	8.67
Myristicaceae	*Otoba parvifolia*	7.14
Lauraceae	*Nectandra longifolia*	5.62
Verbenaceae	*Citharexylum poeppigii*	5.14
Sapindaceae	*Allophylus glabratus*	4.86

Most common species of Mature Floodplain

(includes species without seed sizes)

Yasuni		Trees/ ha	Manu		Trees/ ha
Arecaceae	*Iriartea deltoidea*	30.00	Arecaceae	*Iriartea deltoidea*	46.31
Fabaceae	*Inga stenoptera/striolata cf.*	12.83	Arecaceae	*Astrocaryum murumuru*	38.73
Apocynaceae	*Aspidosperma darienense cf.*	9.33	Myristicaceae	*Otoba parvifolia*	31.08
Lecythidaceae	*Gustavia longifolia*	8.83	Arecaceae	*Attalea butyracea*	25.99
Sapotaceae	*Pouteria "tenuipetiole"*	8.33	Bombacaceae	*Quararibea wittii*	21.00
Fabaceae	*Pterocarpus amazonum-rohrii cf.*	7.67	Arecaceae	*Euterpe precatoria*	14.32
Arecaceae	*Astrocaryum murumuru*	7.50	Arecaceae	*Socratea exorrhiza*	14.32
Annonaceae	*Duguetia spixiana*	7.17	Malvaceae	*Theobroma cacao*	13.87
Lecythidaceae	*Eschweilera coriacea cf.*	7.17	Moraceae	*Pseudolmedia laevis*	13.19
Fabaceae	*Brownea grandiceps*	6.83	Meliaceae	*Guarea macrophylla*	10.98
Moraceae	*Sorocea steinbachii*	6.67	Euphorbiaceae	*Sagotia racemosa*	6.79
Violaceae	*Rinorea viridifolia*	6.50	Violaceae	*Leonia glycycarpa*	6.28
Malvaceae	*Apeiba aspera*	6.33	Annonaceae	*Oxandra acuminata*	6.06
Meliaceae	*Guarea guidonia cf.*	6.33	Fabaceae	*Lonchocarpus spiciflorus*	6.06
Myristicaceae	*Virola pavonis*	6.33	Ulmaceae	*Celtis schippii*	6.00

Most common species of Terra Firme

(includes species without seed sizes)

Yasuni		Trees/ ha	Manu		Trees/ ha
Arecaceae	*Iriartea deltoidea*	49.13	Arecaceae	*Iriartea deltoidea*	51.96
Malvaceae	*Matisia malacocalyx*	15.80	Moraceae	*Pseudolmedia laevis*	17.15
Violaceae	*Rinorea apiculata*	12.33	Violaceae	*Leonia glycycarpa*	11.74
Fabaceae	*Brownea grandiceps*	9.60	Arecaceae	*Euterpe precatoria*	11.15
Lecythidaceae	*Grias neuberthii*	9.00	Malvaceae	*Theobroma cacao*	9.22
Lecythidaceae	*Eschweilera coriacea cf.*	8.40	Arecaceae	*Astrocaryum murumuru*	8.63
Monimiaceae	*Siparuna decipiens*	6.60	Violaceae	*Rinorea guianensis*	8.26
Lecythidaceae	*Gustavia longifolia*	6.47	Arecaceae	*Attalea butyracea*	7.44
Moraceae	*Pseudolmedia laevis*	6.47	Moraceae	*Pseudolmedia macrophylla*	6.67
Myristicaceae	*Otoba glycycarpa*	6.27	Euphorbiaceae	*Pausandra trianae*	6.59
Urticaceae	*Pourouma bicolor*	5.93	Urticaceae	*Pourouma minor*	6.59
Malvaceae	*Apeiba aspera*	5.33	Ulmaceae	*Celtis schippii*	6.44
Malvaceae	*Matisia obliquifolia*	5.27	Violaceae	*Rinorea viridifolia*	6.04
Moraceae	*Perebea xanthochyma*	4.73	Bombacaceae	*Quararibea wittii*	5.96
Myristicaceae	*Otoba parvifolia cf.*	4.73	Moraceae	*Pseudolmedia laevigata*	5.70

Most common species of Swamp

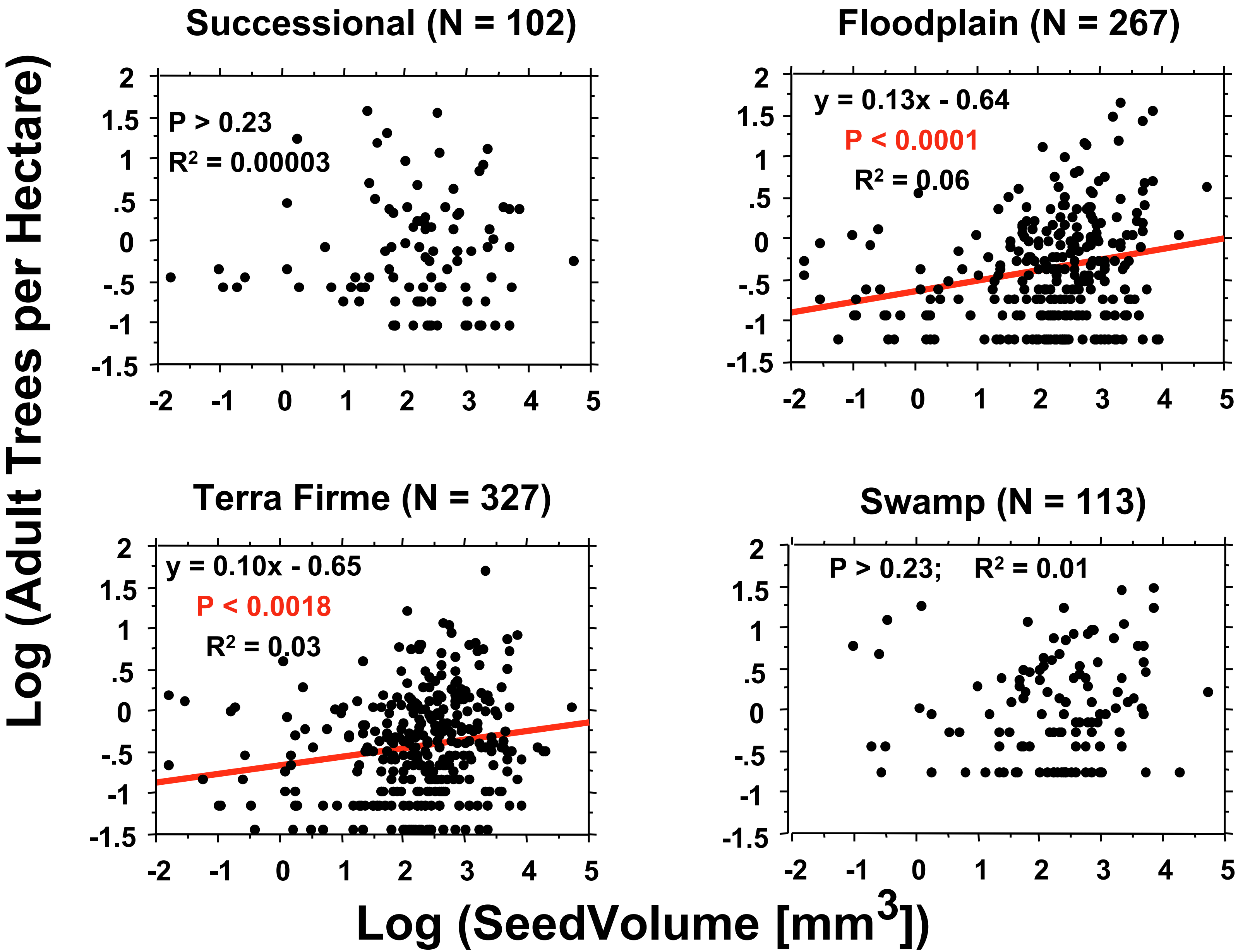
(includes species without seed sizes)

Yasuni		Trees/ ha	Manu		Trees/ ha
Arecaceae	*Mauritiella armata*	75.60	Flacourtiac.	*Laetia corymbulosa*	40.00
Arecaceae	*Mauritia flexuosa*	71.80	Arecaceae	*Mauritia flexuosa*	31.09
Arecaceae	*Iriartea deltoidea*	68.60	Arecaceae	*Iriartea deltoidea*	28.91
Arecaceae	*Euterpe precatoria*	65.40	Sapindac.	*Allophylus scrobiculatus*	23.64
Arecaceae	*Attalea butyracea*	29.20	Fabaceae	*Lonchocarpus spiciflorus*	21.45
Fabaceae	*Macrolobium angustifolium cf.*	26.20	Malvaceae	*Guazuma crinita*	18.73
Arecaceae	*Oenocarpus bataua*	15.20	Fabaceae	*Zygia latifolia*	17.82
Fabaceae	*Zygia "gold"*	10.80	Arecaceae	*Astrocaryum murumuru*	17.27
Elaeocarpac.	*Sloanea "bark"*	10.40	Moraceae	*Ficus trigona*	12.73
Euphorbiac.	*Hyeronima alchorneoides*	9.00	Fabaceae	*Inga nitida*	12.18
Arecaceae	*Socratea exorrhiza*	8.80	Annonac.	*Xylopia ligustrifolia*	12.00
Polygonaceae	*Triplaris americana aff.*	7.80	Clusiaceae	*Calophyllum brasiliense*	11.27
Salicaceae	*Casearia uleana cf.*	6.80	Meliaceae	*Trichilia pleeana*	9.64
Arecaceae	*Astrocaryum murumuru*	6.00	Annonaceae	*Unonopsis floribunda*	9.27
Fabaceae	*Pterocarpus amazonum-rohrii cf.*	6.00	Fabaceae	*Inga ruiziana*	8.36

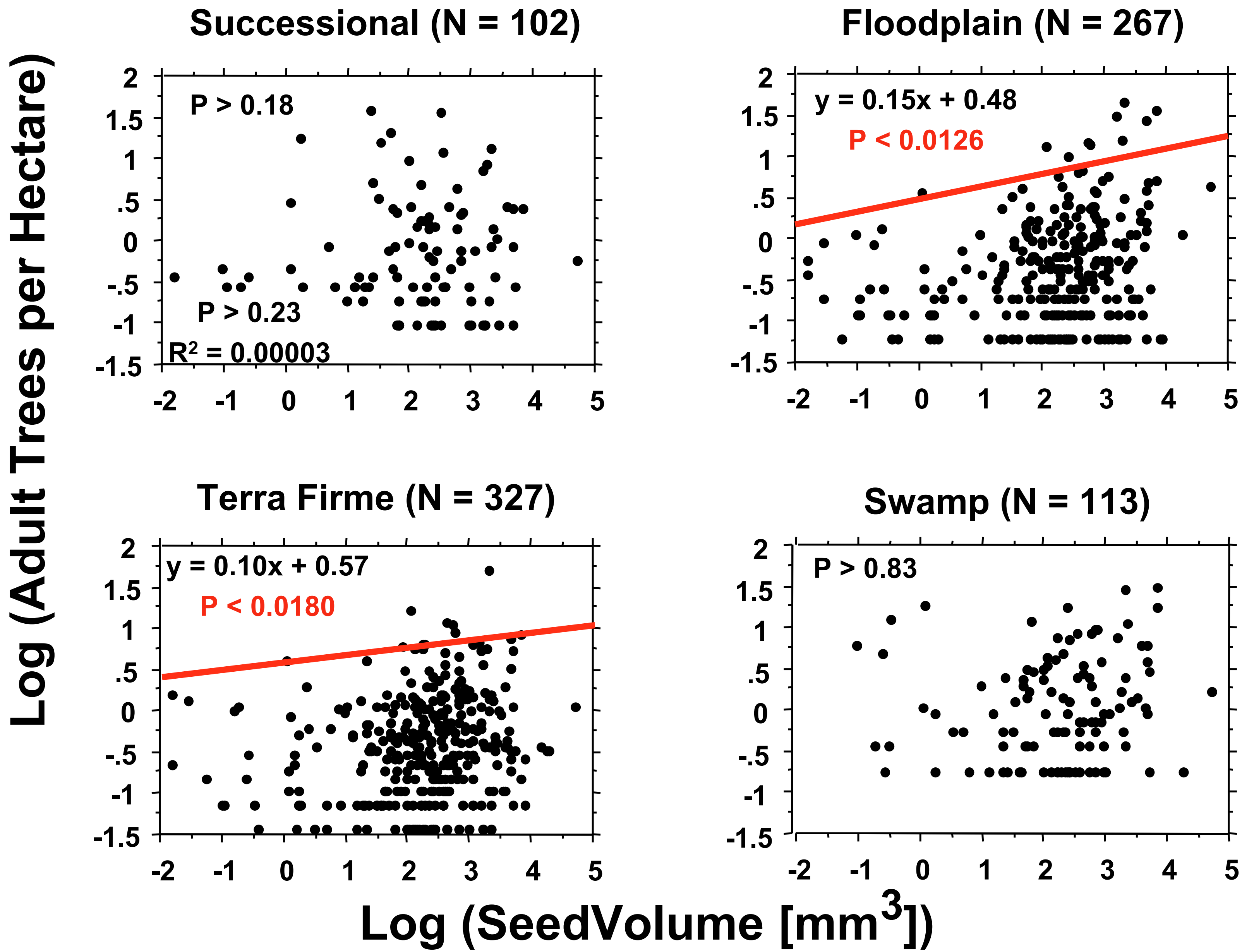
Detecting the *Ecological* function of seed size

- Does seed size affect performance within tropical species?
- **Does seed size predict abundances of adult trees within habitats?**
- Do species sort themselves among habitats on the basis of seed size?
- Does seed size predict habitat preferences?

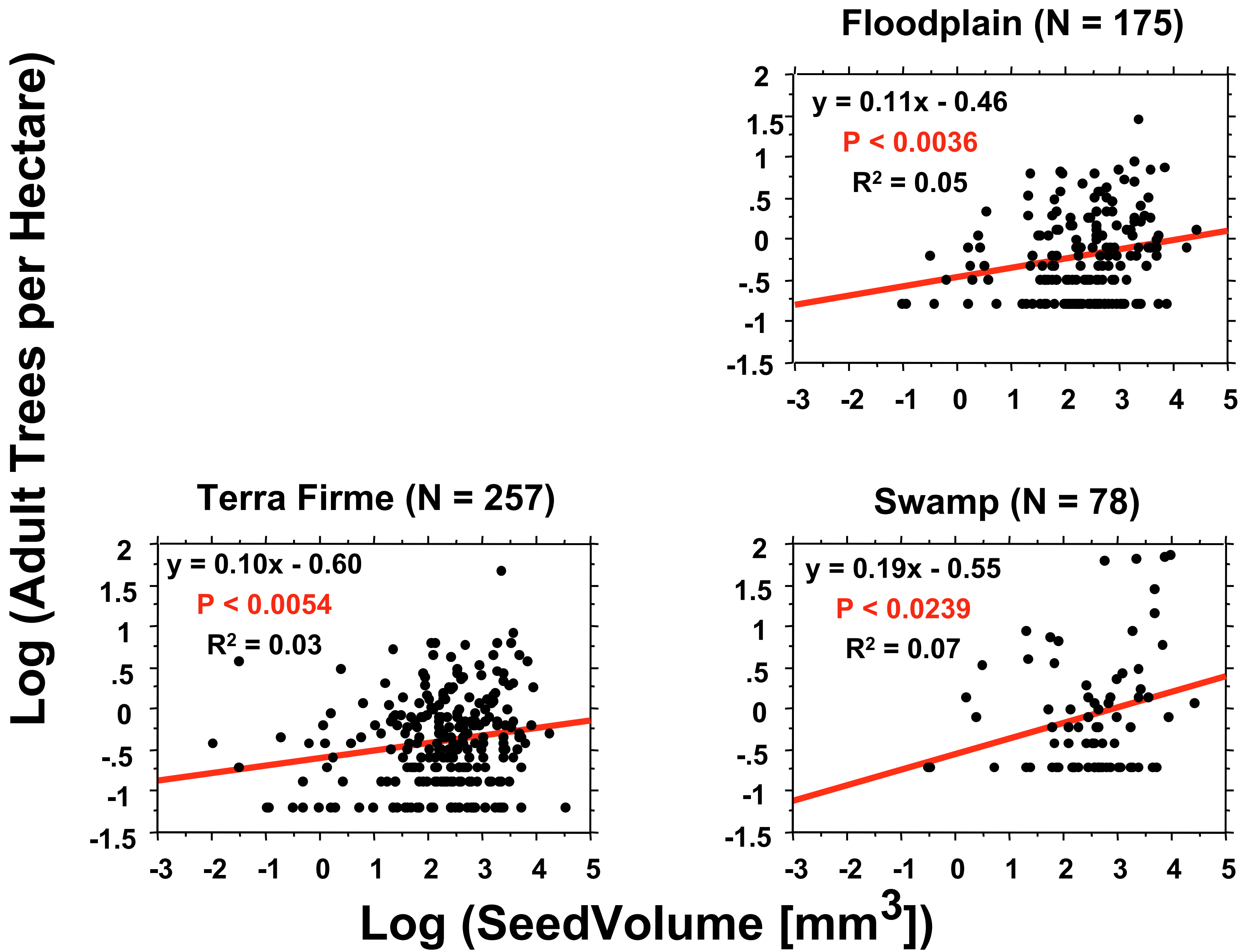
Manu, Peru: Ordinary Least Squares Regression



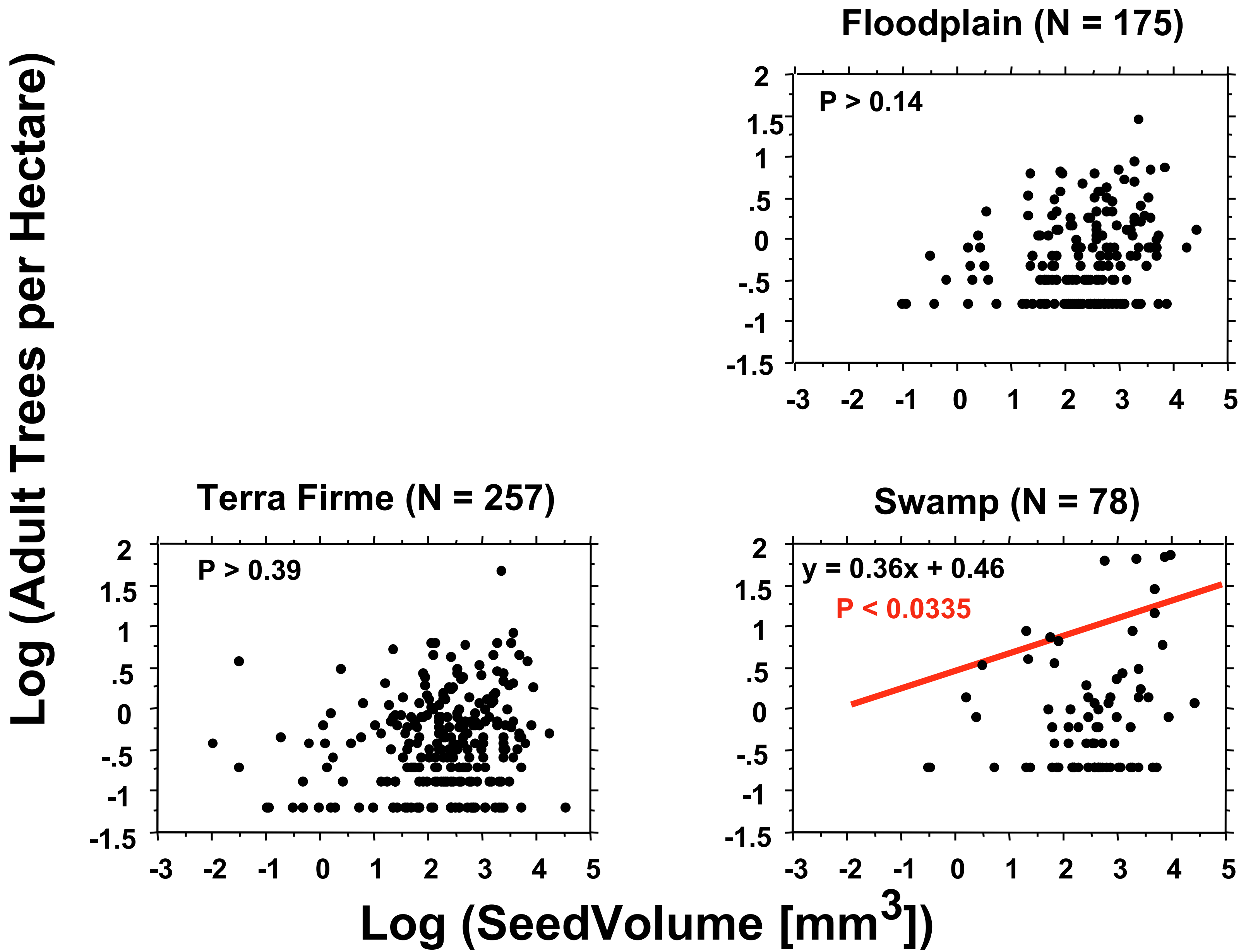
Manu, Peru: 95th Quantile Regression



Yasuni, Ecuador: Ordinary Least Squares Regression



Yasuni, Ecuador: 95th Quantile Regression

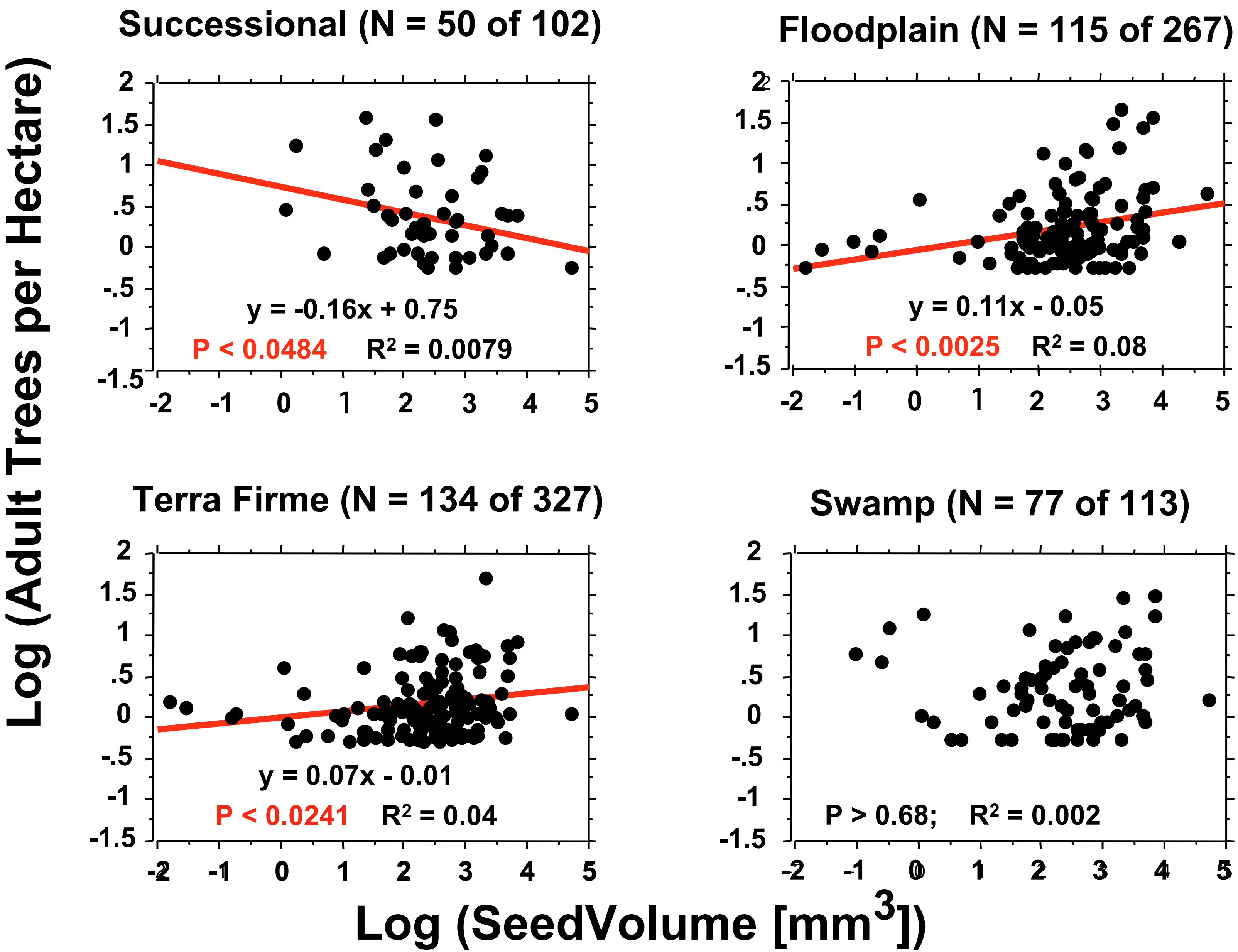


Summary of least squares regressions

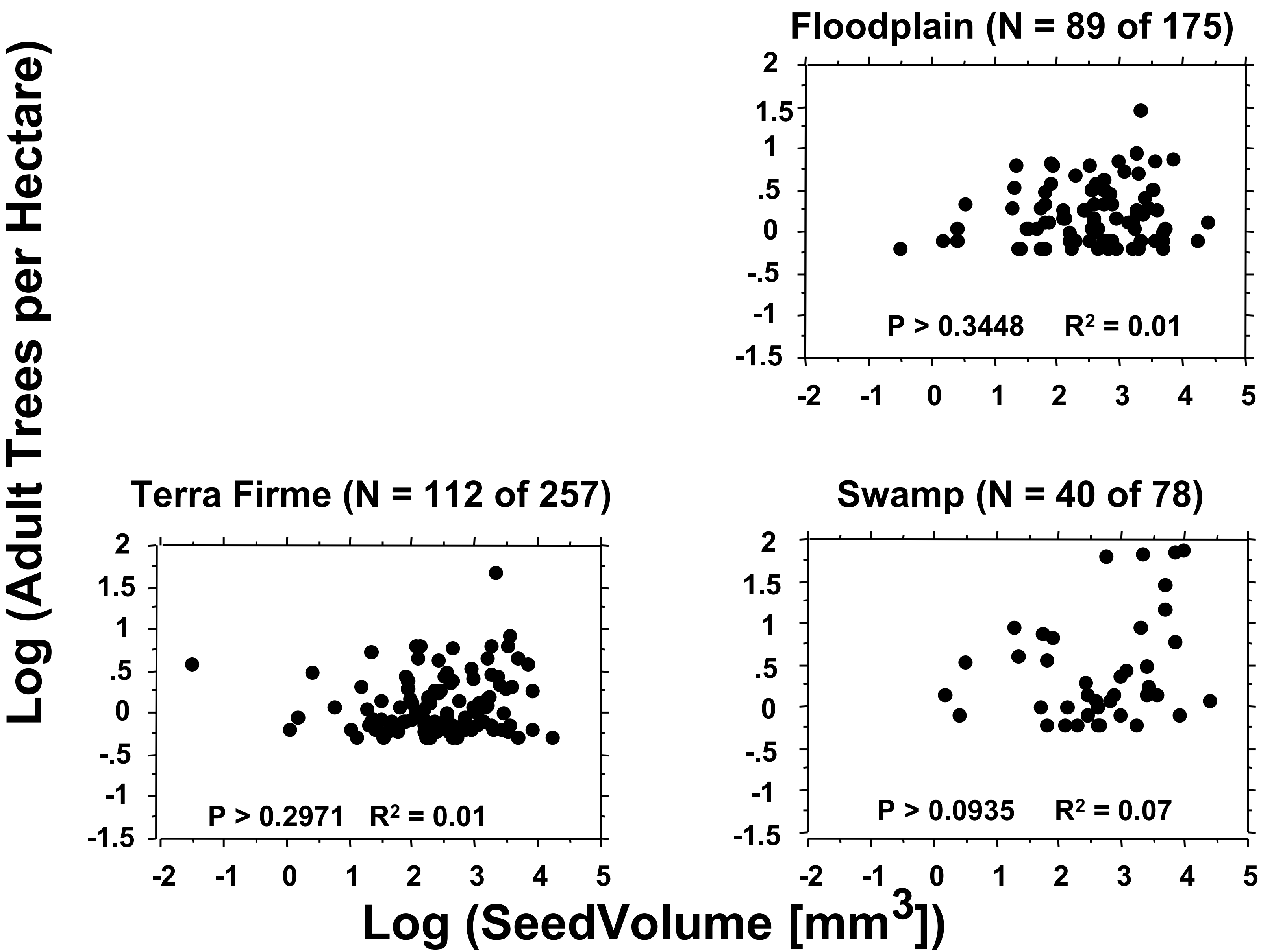
log (adult density) vs. log (seed volume)

Region	Habitat	Regression equation	P-value	N
Manu	Successional		ns	102
Manu	**Floodplain**	**y = 0.13x - 0.64**	**< 0.0001**	**267**
Manu	**Terra Firme**	**y = 0.10x - 0.65**	**< 0.0018**	**327**
Manu	Swamp		ns	113
Yasuni	**Floodplain**	**y = 0.11x - 0.46**	**< 0.0036**	**175**
Yasuni	**Terra Firme**	**y = 0.09x - 0.60**	**< 0.0054**	**257**
Yasuni	**Swamp**	**y = 0.19x - 0.55**	**< 0.0239**	**78**

Manu, Peru: Densities > 0.5 trees/ha



Yasuni, Ecuador: Densities > 0.5 trees/ha



Detecting the *Ecological* function of seed size

- Does seed size affect performance <u>within</u> species?
- **Does seed size predict tree abundance <u>within</u> habitats?**
  - ✓ **Sometimes, but weakly**
  - ✓ **Mature forest: Large-seeded species dominate in Manu**
  - ✓ **Swamp forest: Large-seeded species dominate in Yasuni**

Detecting the *Ecological* function of seed size

- Does seed size affect performance within species?
- Does seed size predict abundance within habitats?
- **Do species sort themselves among habitats on the basis of seed size?**

Frequency distributions of seed size by habitat

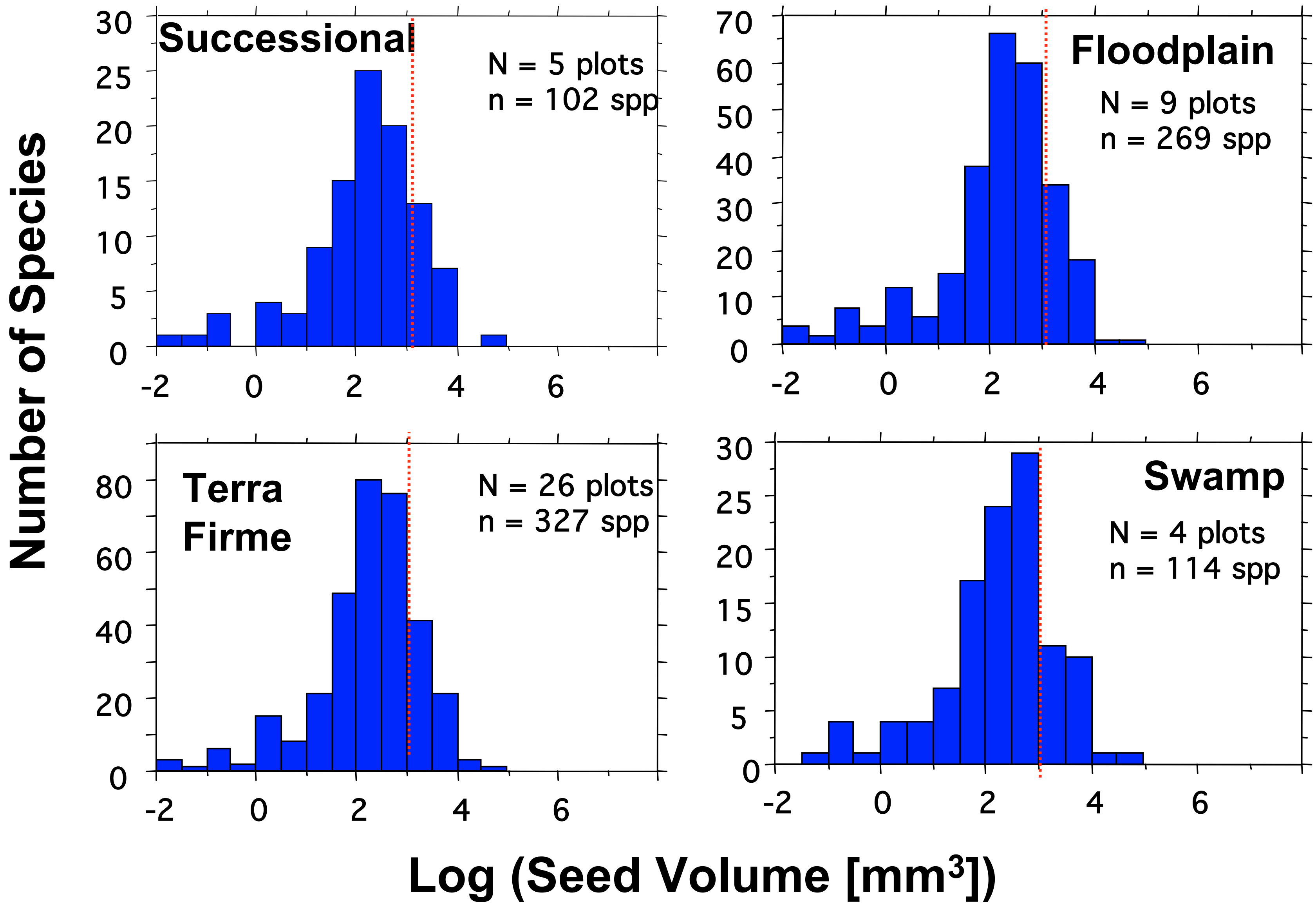
Mean seed size of the species in each habitat

Mean seed size of all individuals in each habitat

Mean seed size of the top 15 species in each habitat

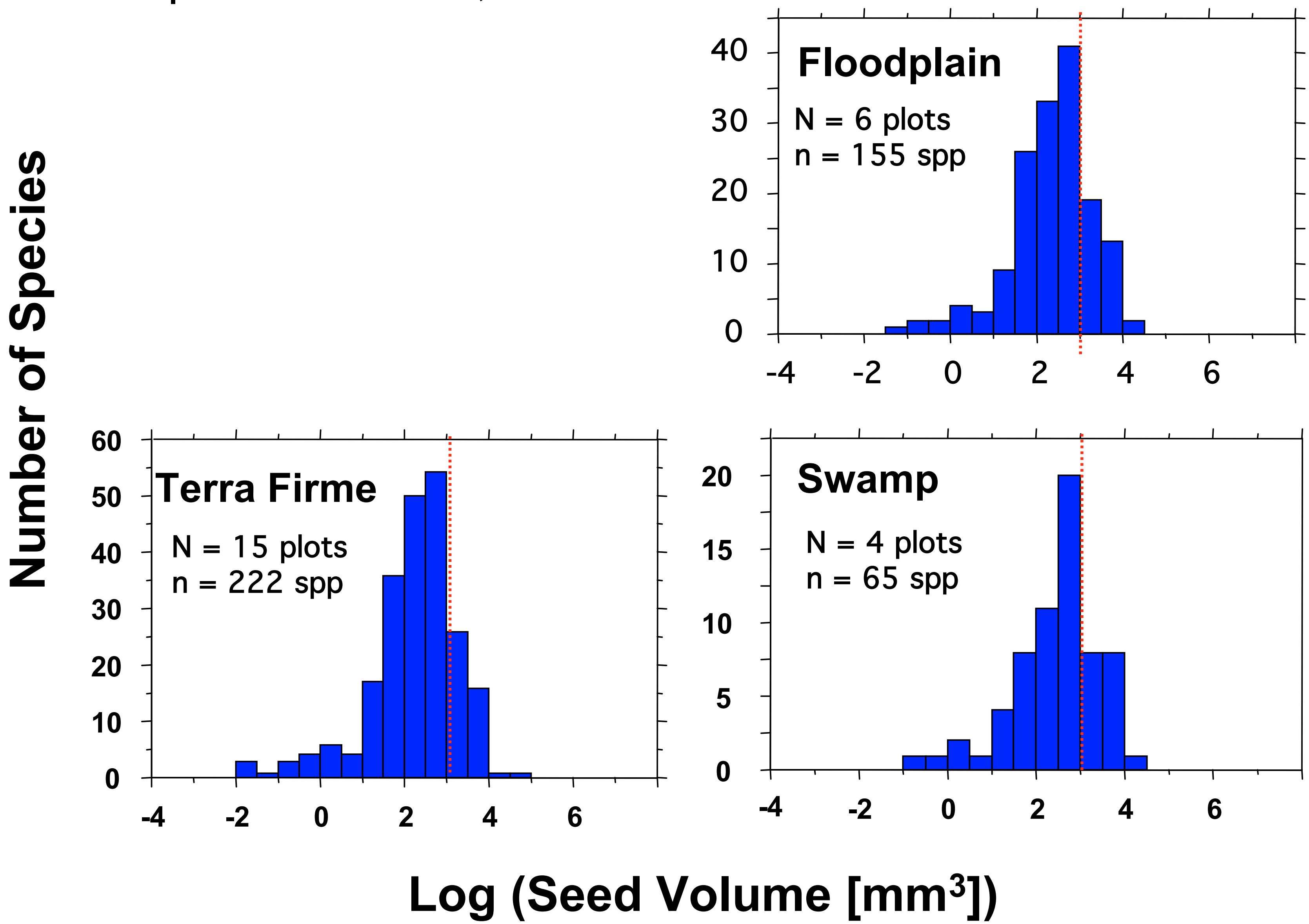
Manu, Peru: Frequency Distributions of Seed Volume

Most species < 1,000 mm^3



Yasuni: Frequency Distributions of Seed Volume

Most species are < 1,000 mm^3



Summary:

Habitats are occupied by species with similar seed size distributions.

Species represent seven orders of magnitude in seed size within habitats.

The modal value of seed size is similar among habitats.

Detecting the *Ecological* function of seed size

- Does seed size affect performance <u>within</u> species?
- Does seed size predict abundance <u>within</u> habitats?
- **Do species sort themselves among habitats on the basis of seed size?**

    Frequency distributions of seed size by habitat

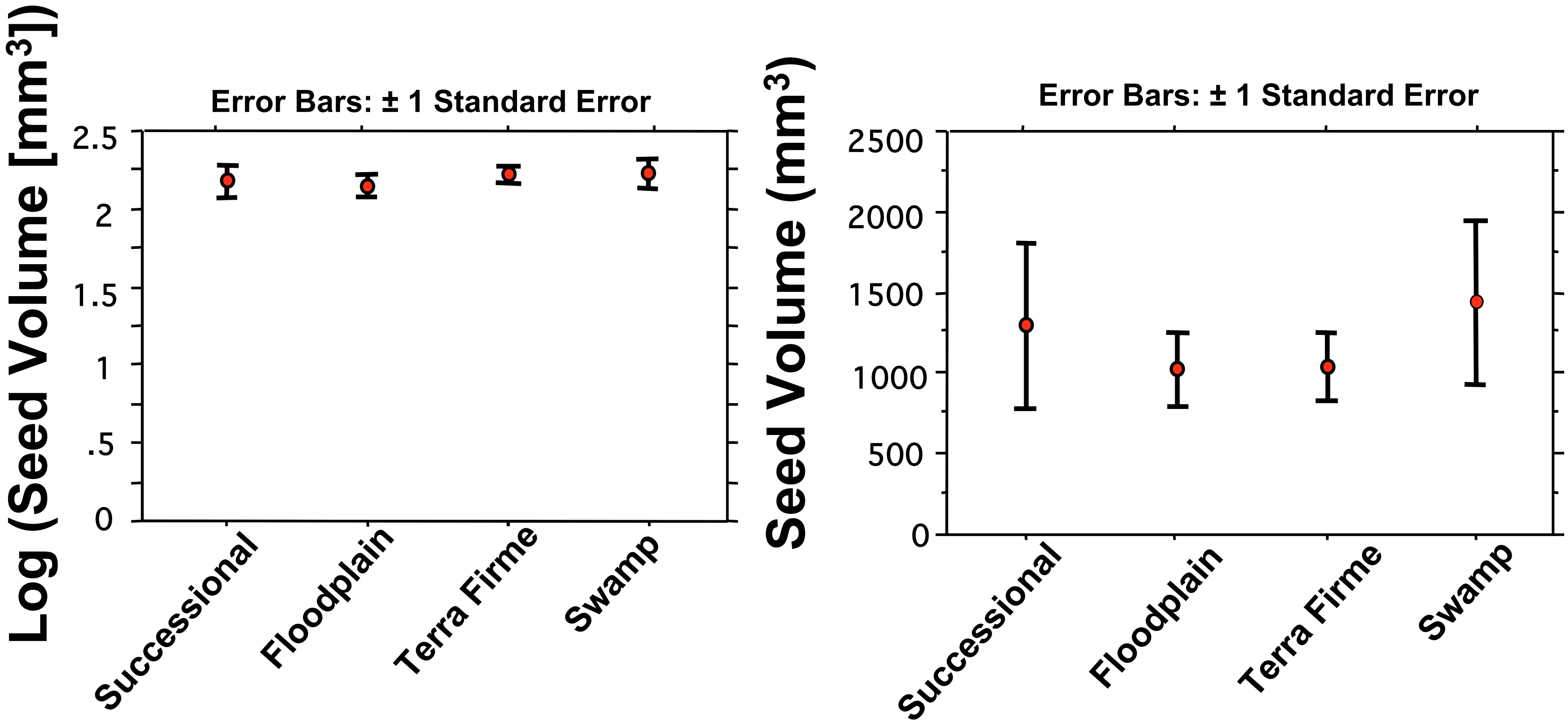
    Mean seed size of the species in each habitat

Manu: Mean Seed Size Among Forest Types

01-2005

ANOVA: Log(SeedVolume)

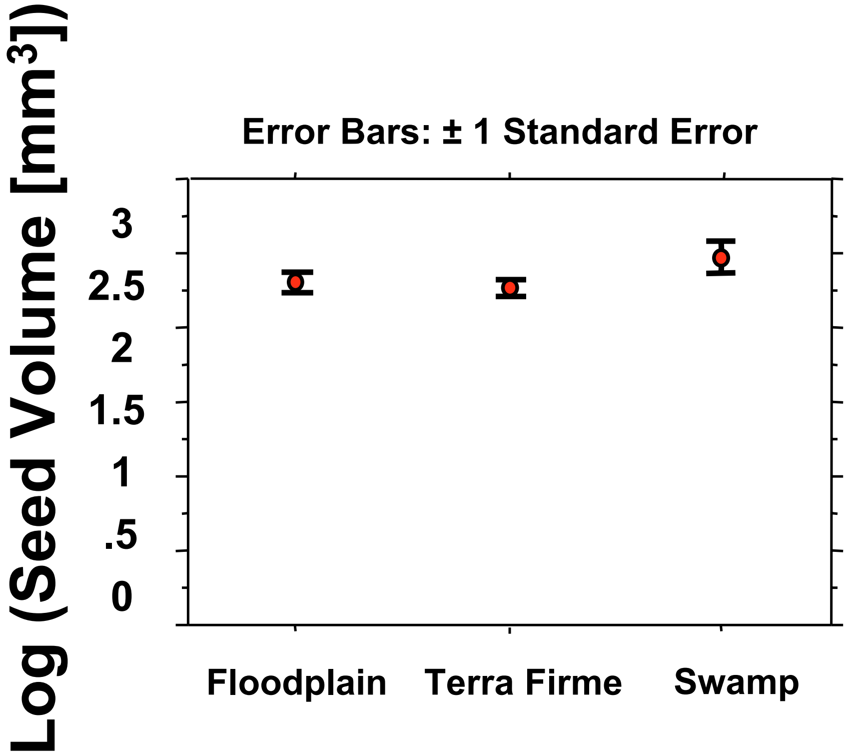
	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Habitat Type	3	1.06	.35	.286	.8359	.857	.104
Residual	805	997.78	1.24				

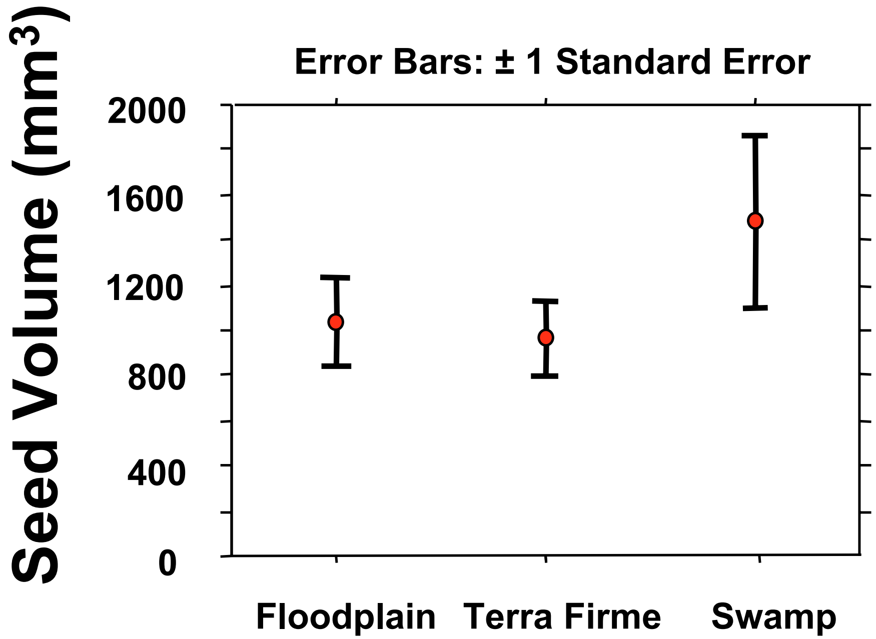


Yasuni: Mean Seed Size Among Forest Types

ANOVA Table for Log(SeedVolume)

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Habitat	2	3.238	1.619	1.588	0.2053	3.177	.324
Residual	507	516.822	1.019				





Summary:

Habitats do not differ in the mean seed size of the species within them

But: These analyses treat all species as equal – they do not take abundance into account

Detecting the *Ecological* function of seed size

- Does seed size affect performance within species?
- Does seed size predict abundance within habitats?
- **Do species sort themselves among habitats on the basis of seed size?**

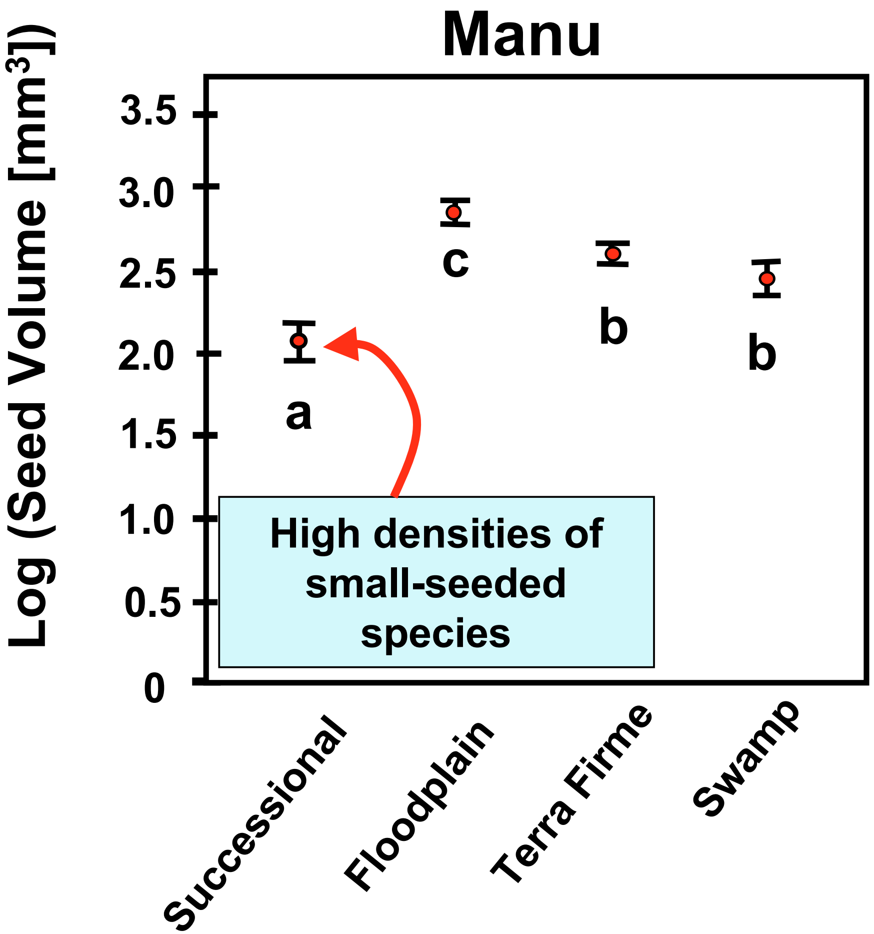
  Frequency distributions of seed size by habitat

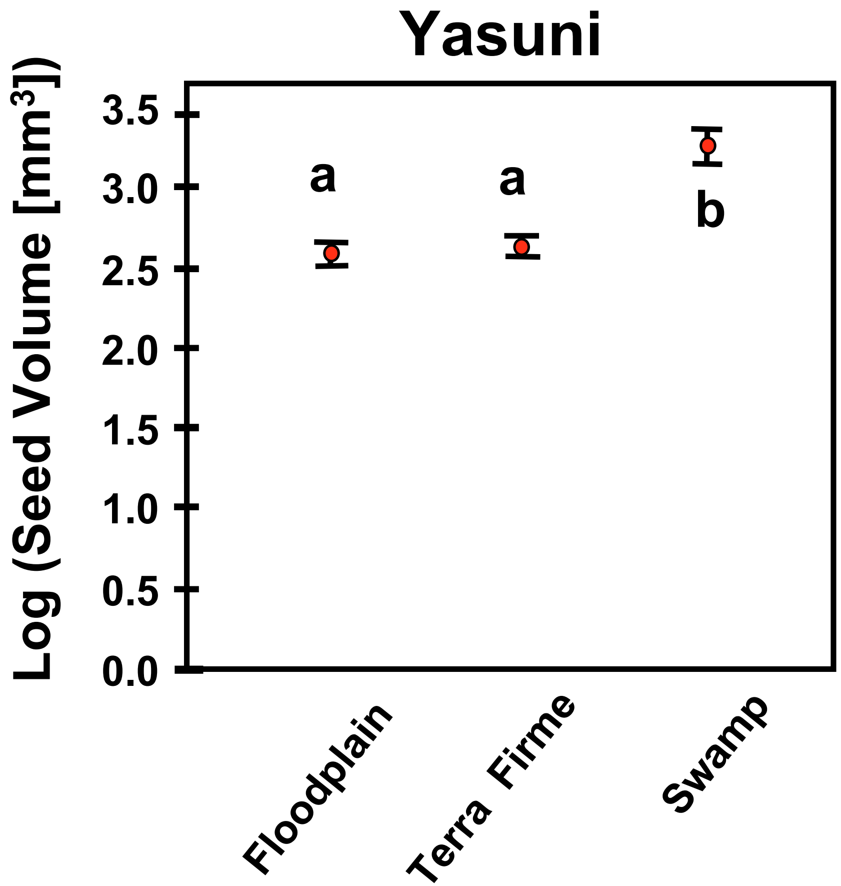
  Mean seed size of the species in each habitat

  Mean seed size of all individuals in each habitat

Weighted ANOVA: Species weighted by their abundance

01-2005



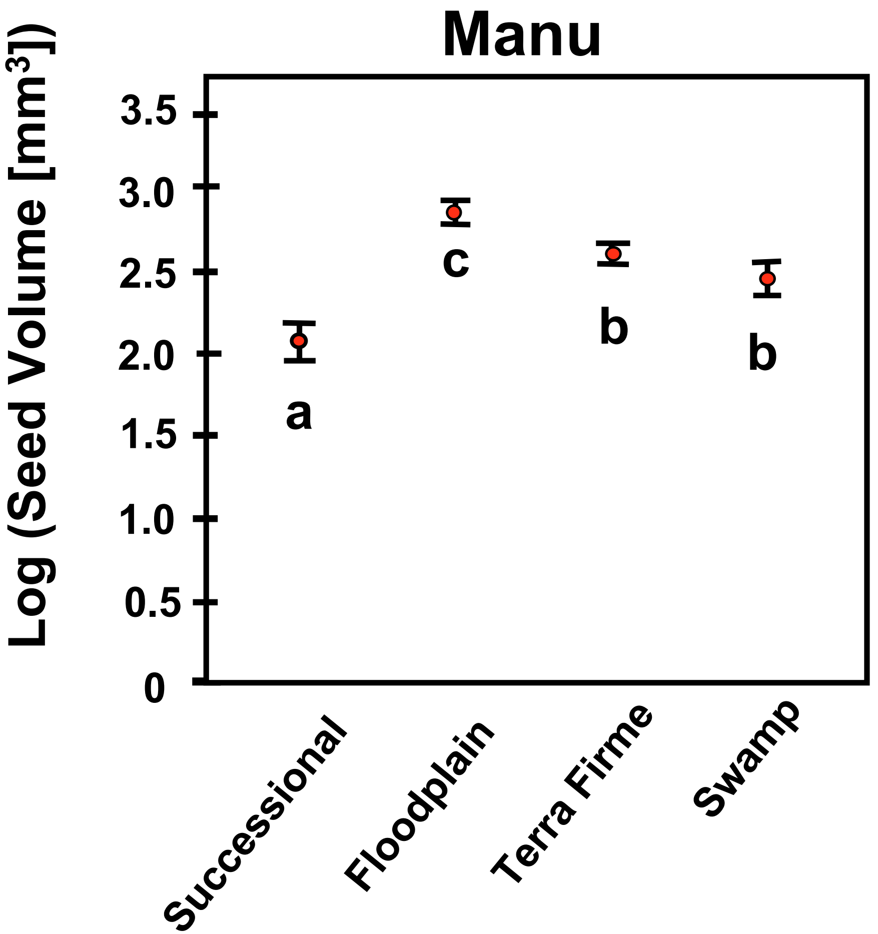


Source	DF	Sum of Squares	Mean Square	F Ratio
Habitat	3	106.89	35.63	19.74
Error	805	1453.34	1.81	**Prob > F**
Total	808	1560.23		<.0001

Source	DF	Sum of Squares	Mean Square	F Ratio
Habitat	2	93.82	46.91	34.83
Error	507	682.84	1.35	**Prob > F**
Total	509	776.65		<.0001

Weighted ANOVA: Species weighted by their abundance

01-2005



Source	DF	Sum of Squares	Mean Square	F Ratio
Habitat	3	106.89	35.63	19.74
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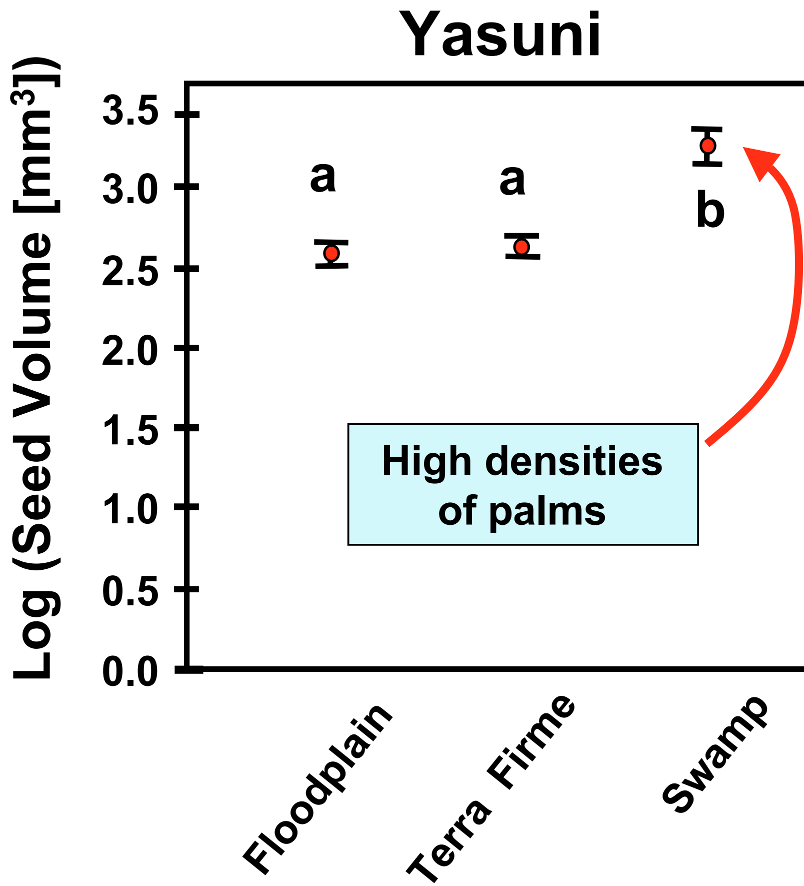
Total	808	1560.23		<.0001



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Habitat	2	93.82	46.91	34.83
Error	507	682.84	1.35	**Prob > F**
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Detecting the *Ecological* function of seed size

- Does seed size affect performance within species?
- Does seed size predict abundance within habitats?
- **Do species sort themselves among habitats on the basis of seed size?**

Frequency distributions of seed size by habitat

Mean seed size of the species in each habitat

Mean seed size of all individuals in each habitat

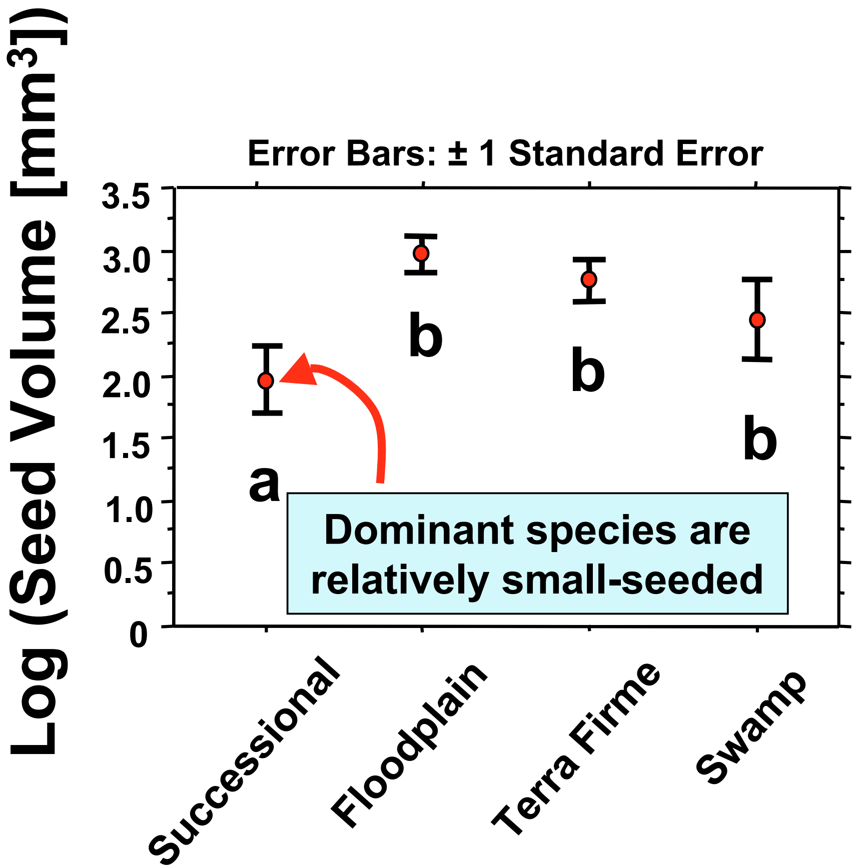
Mean seed size of the top 15 species in each habitat

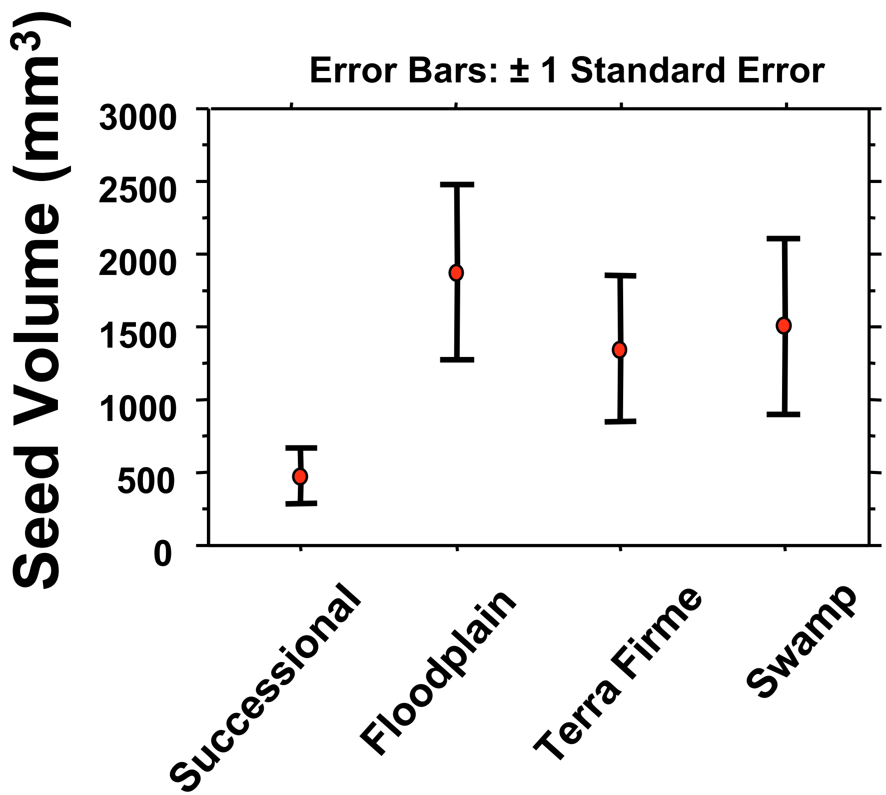
Manu: Mean Seed Size Among Forest Types

02-2005

ANOVA: Log(SeedVolume)

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Habitat	3	8.40	2.80	3.51	.0210	10.53	.754
Residual	56	44.670	.80				





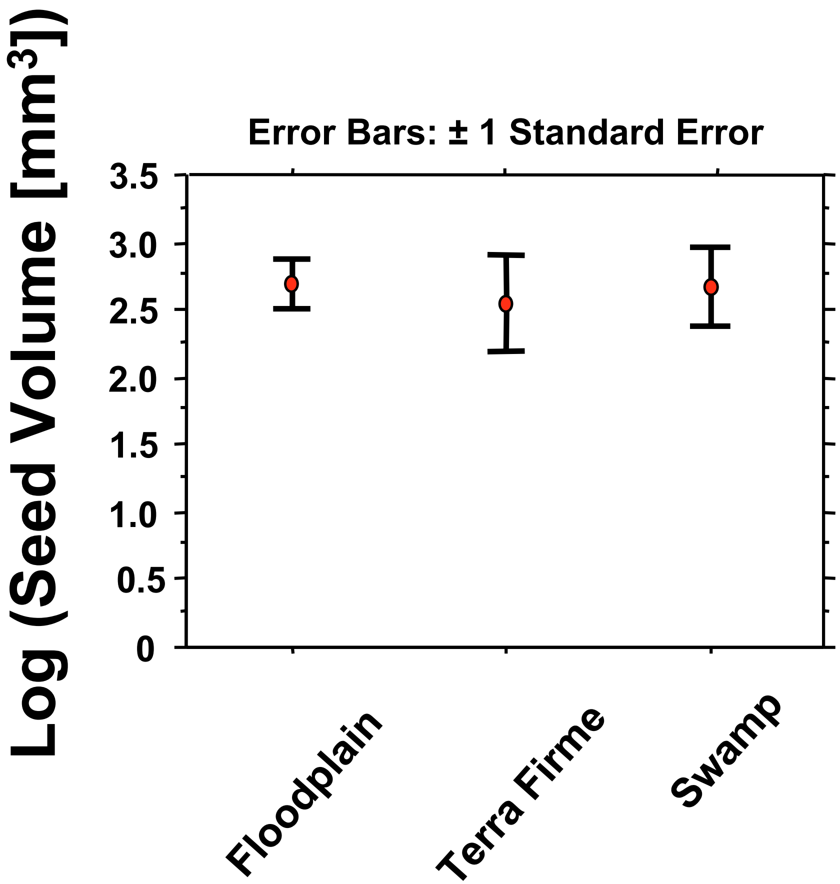
15 Most Abundant Species only

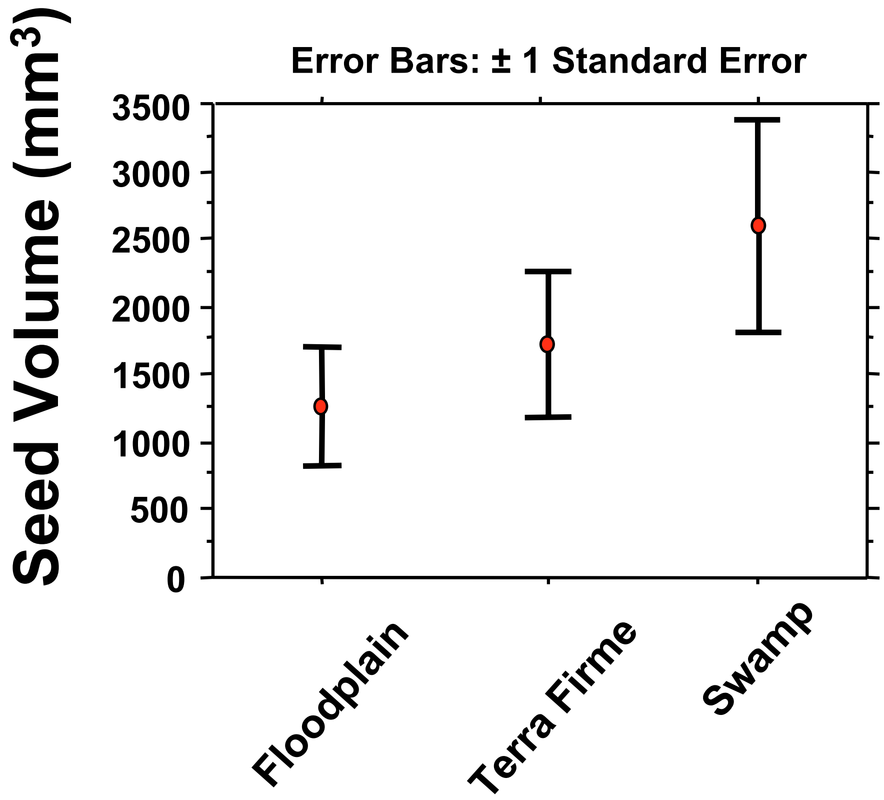
Yasuni: Mean Seed Size Among Forest Types

02-2005

ANOVA: Log(SeedVolume)

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Habitat	2	.164	.082	.069	.9330	.139	.060
Residual	43	50.782	1.181				





15 Most Abundant Species only

Summary

Ecological function of seed size

- Do species sort themselves among habitats on the basis of seed size?

Level of observation	Manu (Peru)	Yasuni (Ecuador)
Mean seed size of all species in each habitat	Habitats do not differ	Habitats do not differ
Mean seed size of all individuals in each habitat	Successional < Mature Forests	Mature Forests < Swamp
Mean seed size of the top 15 species in each habitat	Successional < Mature Forests	Habitats do not differ

Detecting the *Ecological* function of seed size

- Does seed size affect performance within tropical species?
- Does seed size predict abundances of adult trees within habitats?
- Do species sort themselves among habitats on the basis of seed size?
- **Does seed size predict habitat preferences?**

Habitat Preference Index

Species 1

Habitat A (Trees/hectare)

Habitat B (Trees/hectare)

$$\text{Preference Index (A vs. B)} = \frac{\text{Density (Habitat B)}}{\text{Density(B)} + \text{Density(A)}}$$

= 1 if all trees restricted to B

= 0 if all trees restricted to A

$0 \leq \text{Preference Index} \leq 1$

Habitat Preference Index

Species 1

Habitat A
(20 Trees/hectare)

Habitat B
(40 Trees/hectare)

$$\text{Preference Index (A vs. B)} = \frac{40}{60}$$

$$= 0.66$$

$$0 \leq \text{Preference Index} \leq 1$$

Habitat Preference vs. Seed Size

Associations among species

	Manu		Yasuni	
Habitat Preference	**Regression slope**	**P-value**	**Regression slope**	**P-value**
Successional vs. Floodplain	ns	ns		
Successional vs. Terra Firme	+	0.0499		
Successional vs. Swamp	ns	ns		
Floodplain vs. TF	ns	ns	ns	ns
Floodplain vs. Swamp	ns	ns	ns	ns
Terra Firme vs. Swamp	ns	ns	ns	ns

Evidence for the *ecological* function of seed size among species is subtle

- **Habitats do not differ in the mean seed size of their species.**
- **Where seed size predicts abundance, large-seeded species are more abundant than small-seeded species.**
- **Habitats do differ in the mean seed size of the adult *individuals* found within them.**
- **In Manu: habitats differ in the mean seed size of the 15 most abundant species.**
- **Seed size does not predict pairwise habitat preferences.**

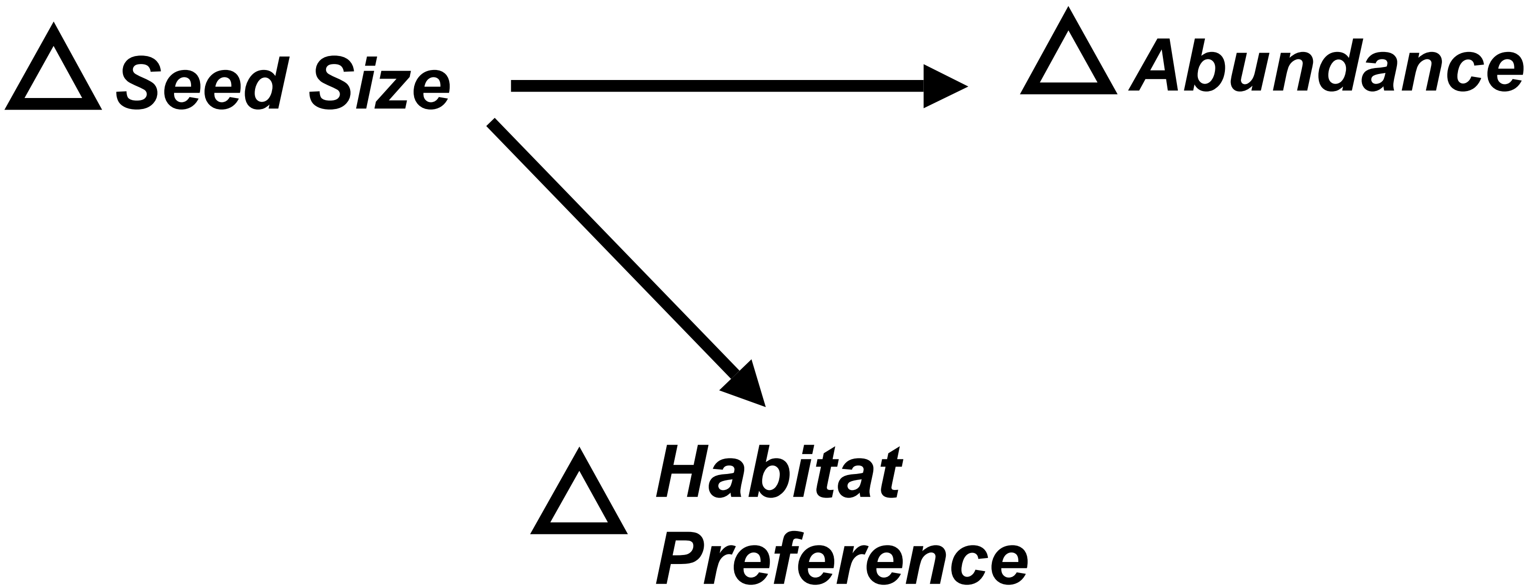
Detecting the *Evolutionary* significance of seed size variation

- **Is evolutionary divergence in seed size associated with differences in abundance within habitats?**
- **Is evolutionary divergence in seed size associated with differences in habitat preference?**

Objective: To control statistically for similarities among large numbers of closely related species that contribute disproportionately to the patterns detected across all species.

Approach: Compare sister taxa with respect to seed size, abundance, and habitat preferences

Testing predictions associated with seed size *evolution*



David Ackerly

Cam Webb

Phylocom

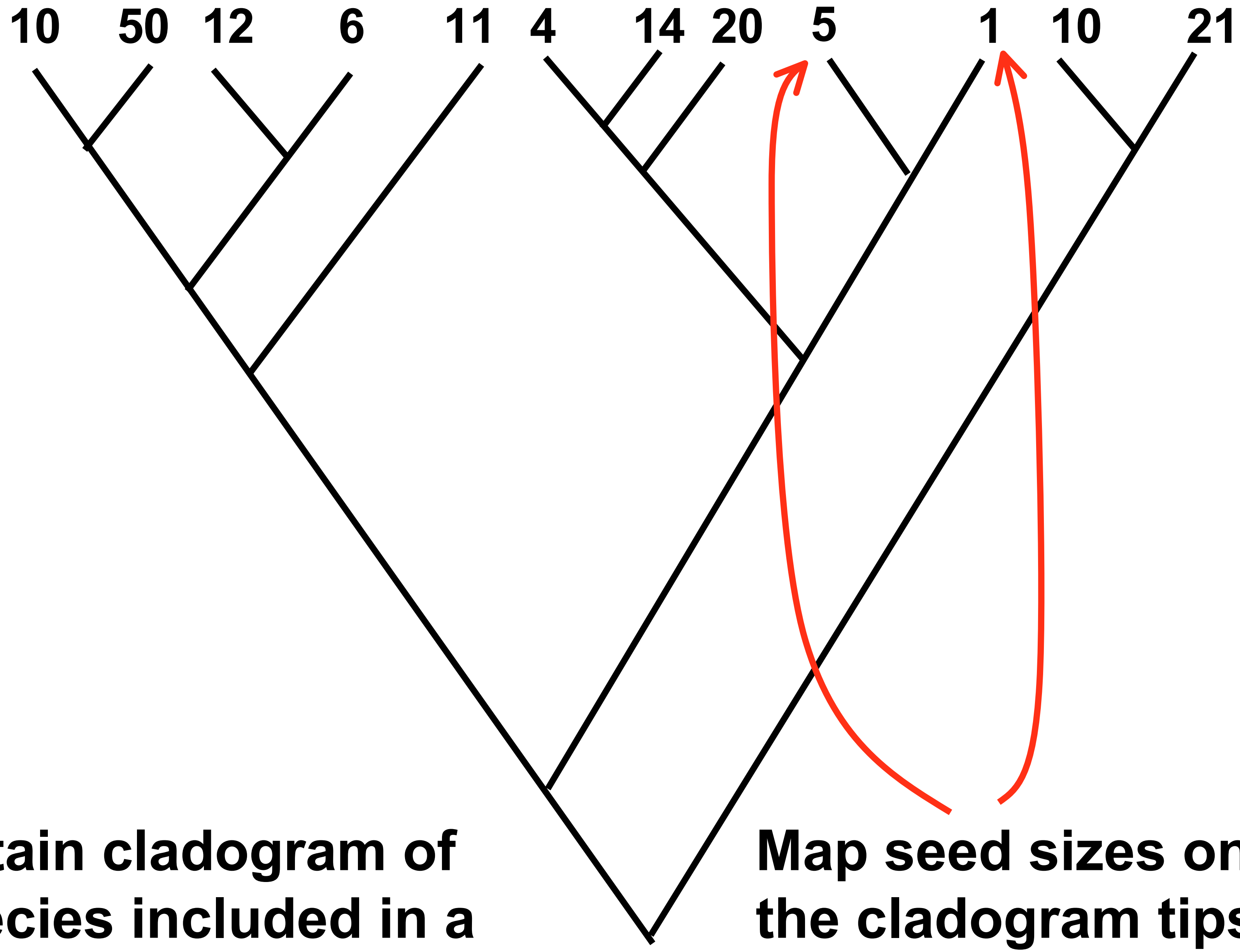
phylomatic
webb
ackerly
kembel

Software for the Analysis of Community Phylogenetic Structure and Character Evolution

Cam Webb, David Ackerly, Steve Kembel

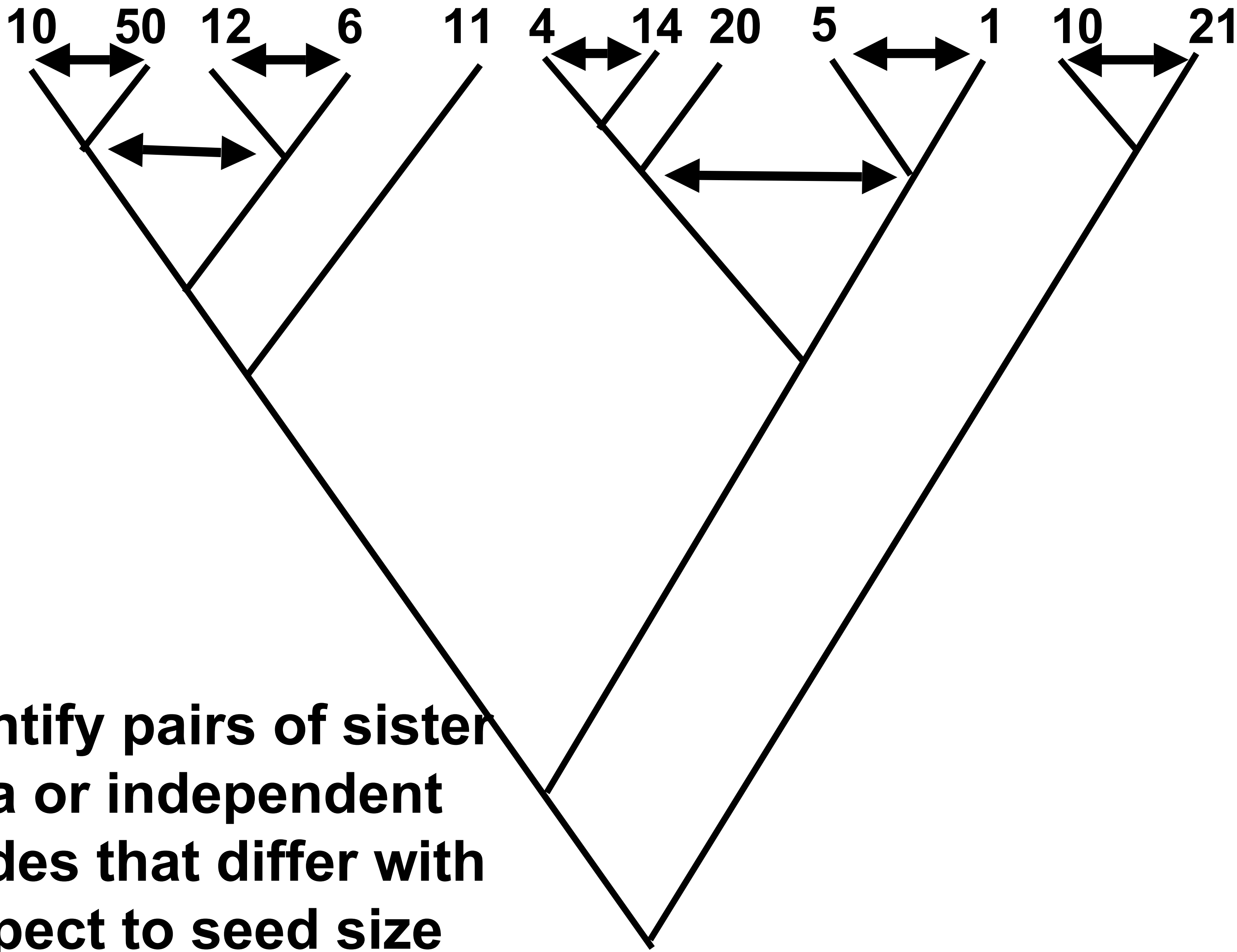
Current Version: 3.22

http://www.phylodiversity.net/phylocom/

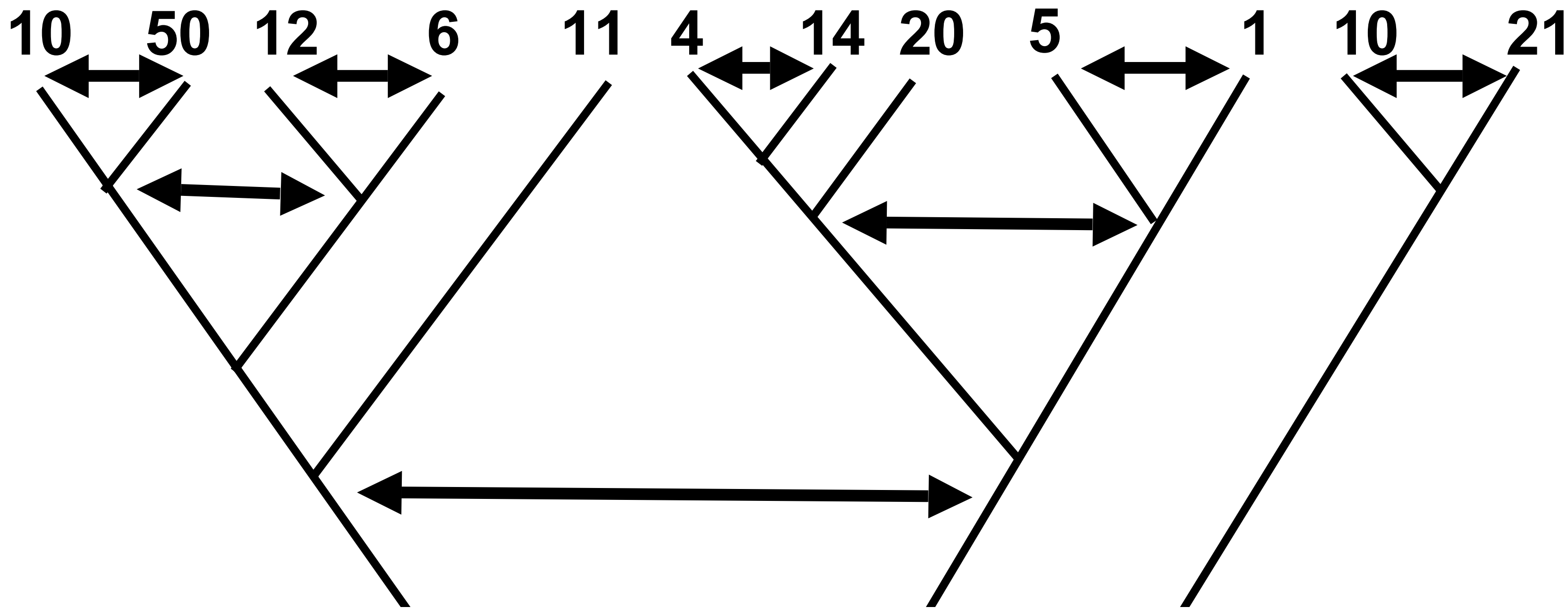


Obtain cladogram of species included in a given habitat

Map seed sizes onto the cladogram tips (cubic millimeters)



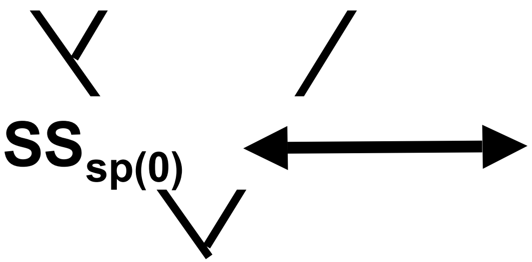
Identify pairs of sister taxa or independent clades that differ with respect to seed size



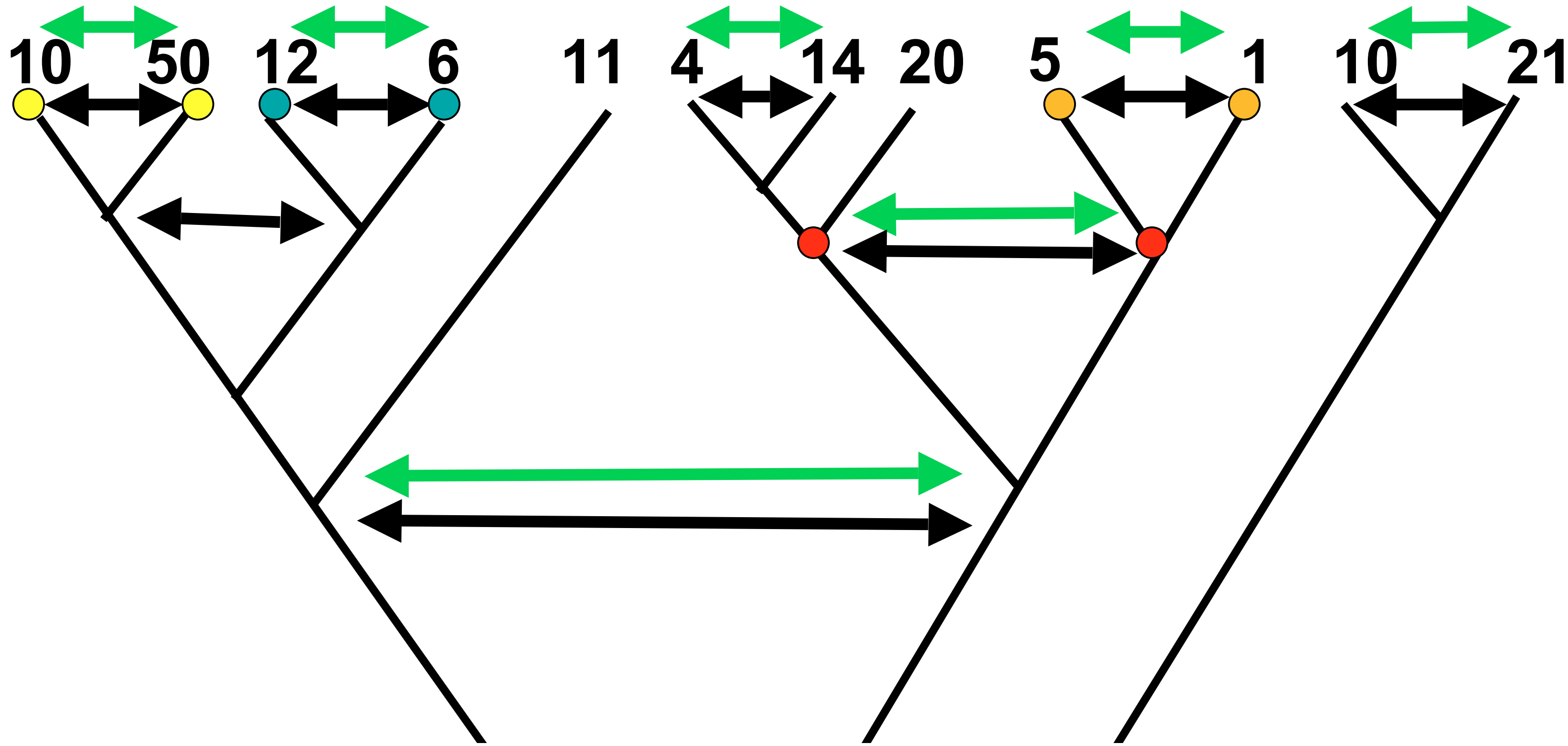
Calculate contrasts for seed size = difference in seed size between sister taxa or between nodes derived from a common ancestor

Conduct all subtractions so that seed size contrasts > 0

Δ Seed Size = $SS_{sp(1)} - SS_{sp(0)}$



= “phylogenetically independent contrasts” = PICS



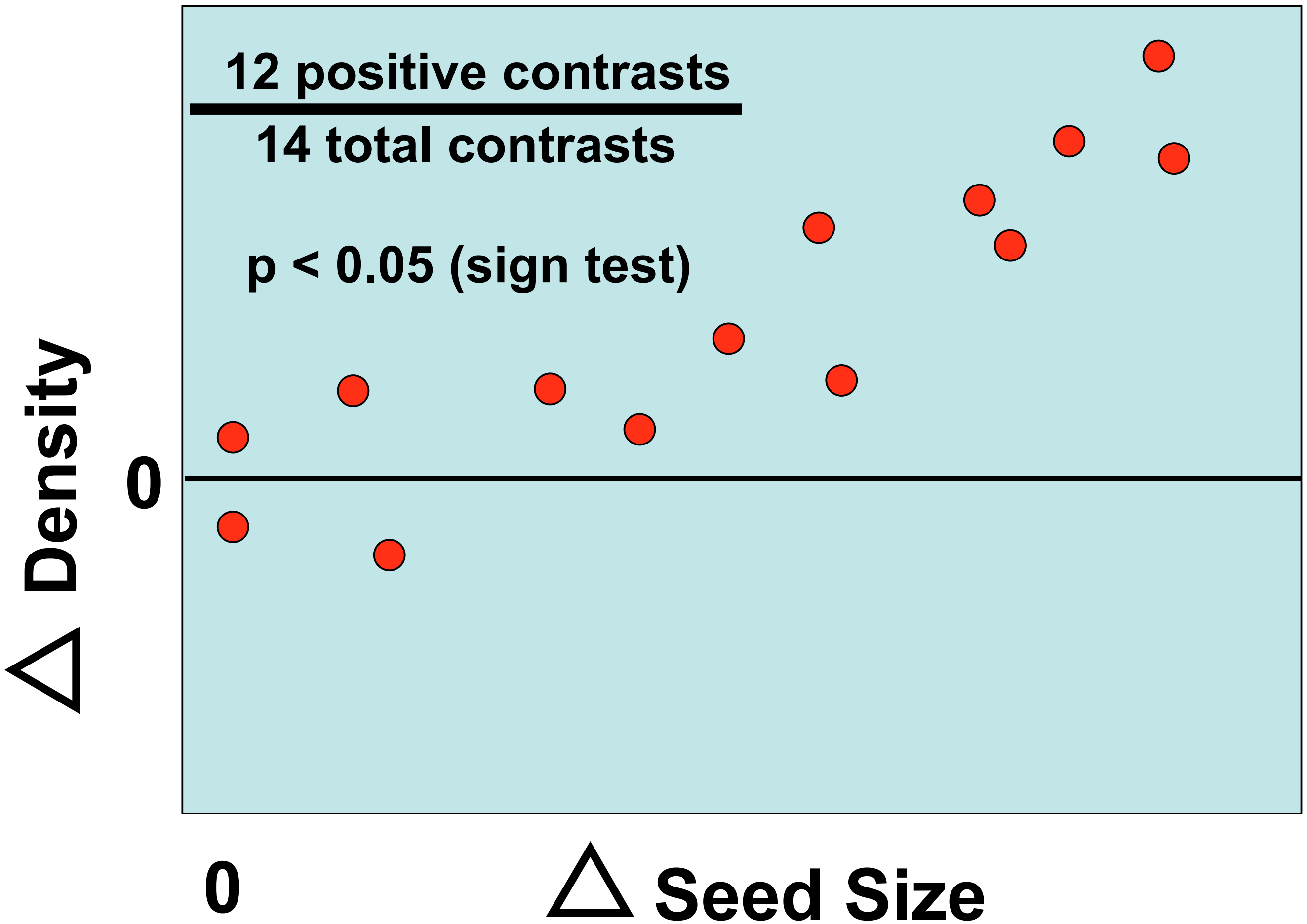
Calculate contrasts for density (or other dependent trait)

Contrasts of the dependent trait may be > 0 or < 0

△ Seed Size = $SS_{sp(1)} - SS_{sp(0)}$

△ Density = $Dens_{sp(1)} - Dens_{sp(0)}$

Plot contrasts: △ Density vs. △ Seed Size



Detecting the *Evolutionary* significance of seed size variation

- **Is evolutionary divergence in seed size associated with differences in abundance within habitats?**

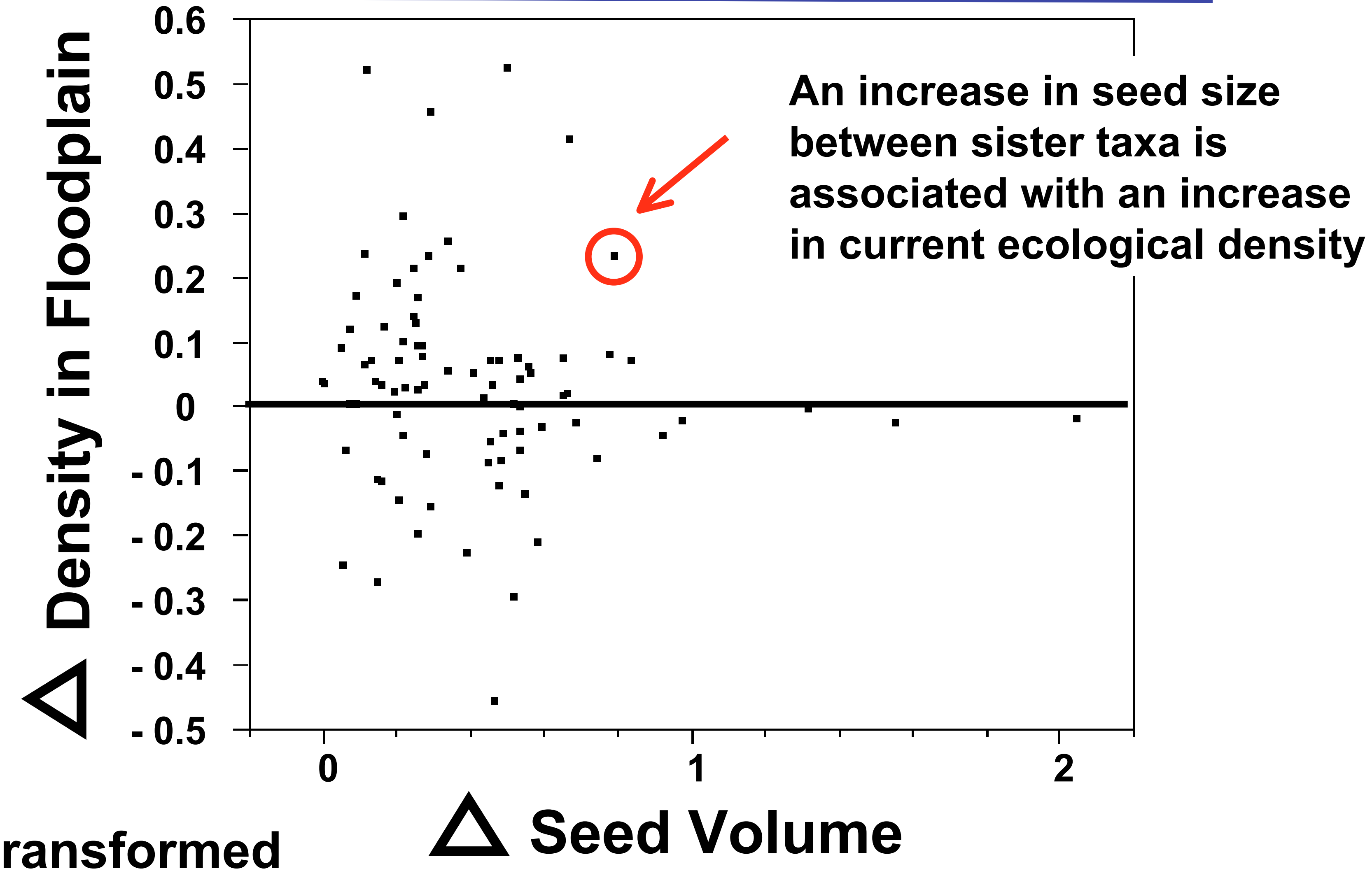
Yasuni, Ecuador

Floodplain: Evolutionary increases in seed size are associated with higher abundances

175 taxa

51/84 contrasts are positive

$p < 0.0315$



log-transformed

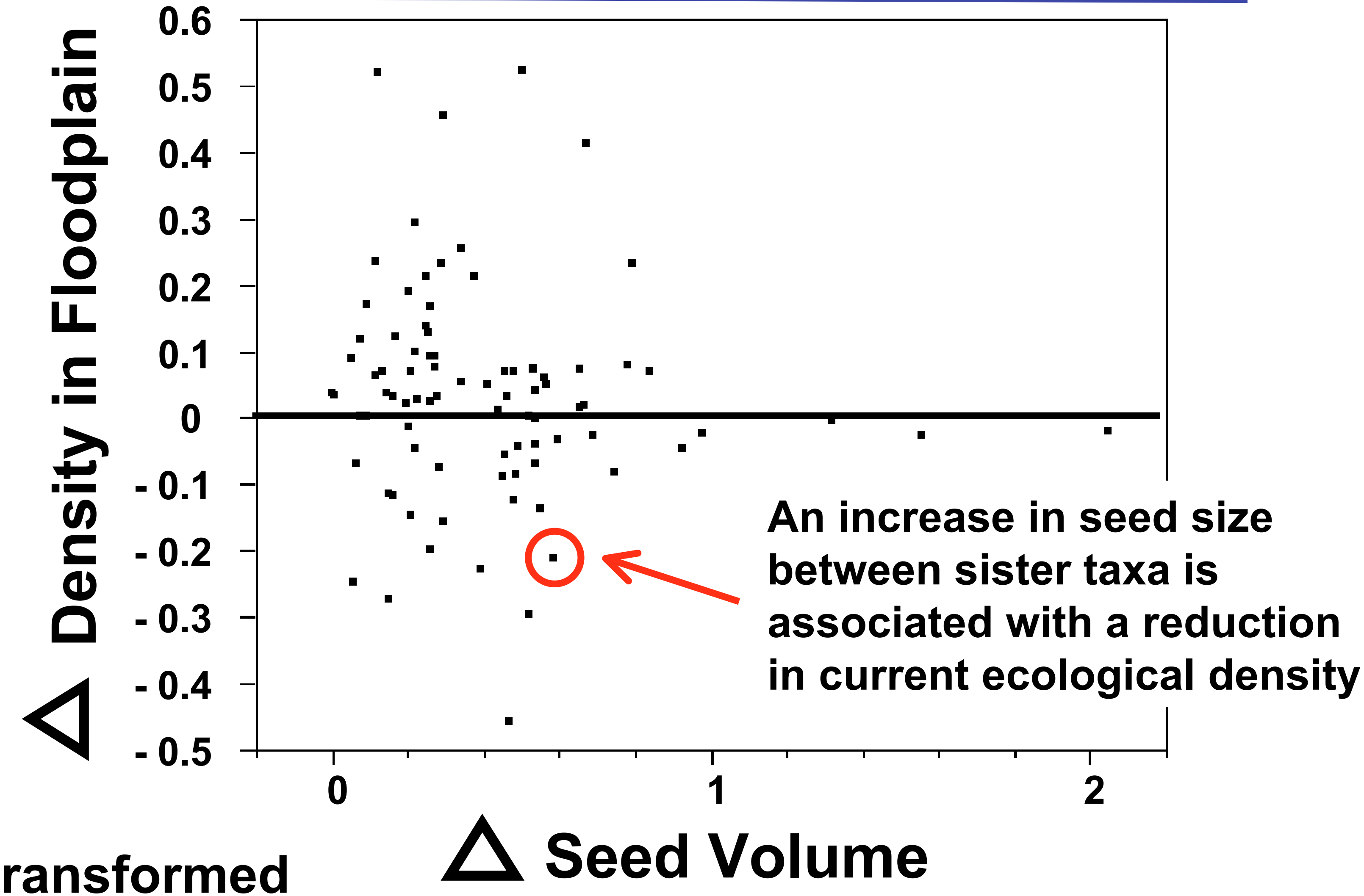
Yasuni, Ecuador

Floodplain: Evolutionary increases in seed size are associated with higher abundances

175 taxa

51/84 contrasts are positive

$p < 0.0315$



log-transformed

Seed Size vs. Abundance

Correlations between phylogenetically independent contrasts (PICS)

← PICS →

Region	Habitat	Sign-test Direction	P-value
Manu	Successional	+	< 0.052
Manu	Floodplain	ns	ns
Manu	Terra Firme	ns	ns
Manu	Swamp	+	< 0.052
Yasuni	Floodplain	+	< 0.032
Yasuni	Terra Firme	ns	ns
Yasuni	Swamp	ns	ns

Seed Size vs. Abundance

Correlations between phylogenetically independent contrasts (PICS) vs. Correlations between species' values (TIPS)

		← PICS →		← TIPS →	
Region	Habitat	Sign-test Direction	P-value	Regression slope	ns
Manu	Successional	+	< 0.052	+	< 0.0001
Manu	Floodplain	ns	ns	+	< 0.0018
Manu	Terra Firme	ns	ns		ns
Manu	Swamp	+	< 0.052	+	< 0.0036
Yasuni	Floodplain	+	< 0.032	+	< 0.0054
Yasuni	Terra Firme	ns	ns	+	< 0.0239
Yasuni	Swamp	ns	ns		ns

Detecting the *Evolutionary* significance of seed size variation

- **Is evolutionary divergence in seed size associated with differences in abundance <u>within</u> habitats?**

✓ **Only weakly, and the "evolutionary" relationships are more difficult to detect than the cross-species relationships.**

Detecting the *Evolutionary* significance of seed size variation

- **Is evolutionary divergence in seed size associated with differences in abundance <u>within</u> habitats?**
- **Is evolutionary divergence in seed size associated with differences in habitat preference?**

  ✓ **Seed size evolution is not accompanied by predictable changes in habitat affinity.**

Summary & Conclusions

Within habitats:

- Seed size predicts the mean and maximum abundances of adult trees in some mature forests
- Seed size alone does not determine species' dominance
- Evolutionary differences in seed size do not reliably predict differences in abundance….

….close relatives do not differ in dominance based on seed size.

Summary & Conclusions

Among habitats:

- **Habitats do not differ in the mean seed size of their species.**
- **Habitats do differ in the mean seed size of their adult individuals.**
- **Seed size does *not* predict habitat preferences among species or between sister taxa**

Evolutionary Implications

Evolutionary divergence in seed size between close relatives does not predict their relative abundances.

…different seed sizes are on average well-adapted to their home environment.

… based on seed size alone, one cannot predict which of two closely related taxa will perform better in a given habitat.

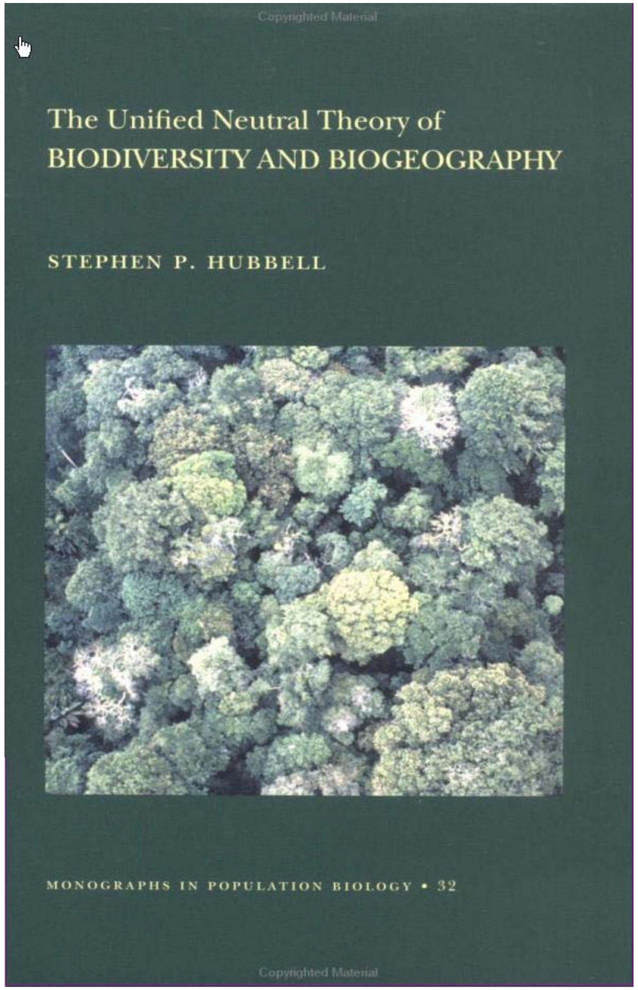
In sum: Seed size is (pretty) neutral

Variation in seed size among coexisting species is very high in spite of positive effects of seed size on seedling performance.

Higher fecundity of small-seeded taxa must compensate for their lower germination and seedling success, particularly in mature forests.

The weak relationship between seed size and adult abundance is reassuring:

If the relationship were strong, it would be much more difficult to explain the persistence of so much variation in seed size.



Future Directions:

- **If seed size doesn't determine the abundances of rainforest trees, does it determine total basal area?**
- **If seed size doesn't determine the distributions and abundances of rainforest trees, what does?**

Future Directions:

- **If seed size doesn't determine the distributions and abundances of rainforest trees, what does?**

  Possibilities:

  Tolerance of local soil type

  Dispersal mechanism & efficacy

  Drought tolerance

  Resistance to habitat-specific diseases/predators

  Distributions of pathogenic and mutualistic fungi and soil microbes

  Pollination requirements