BIODIVERSITY HOTSPOTS HOUSE MOST UNDISCOVERED PLANT SPECIES

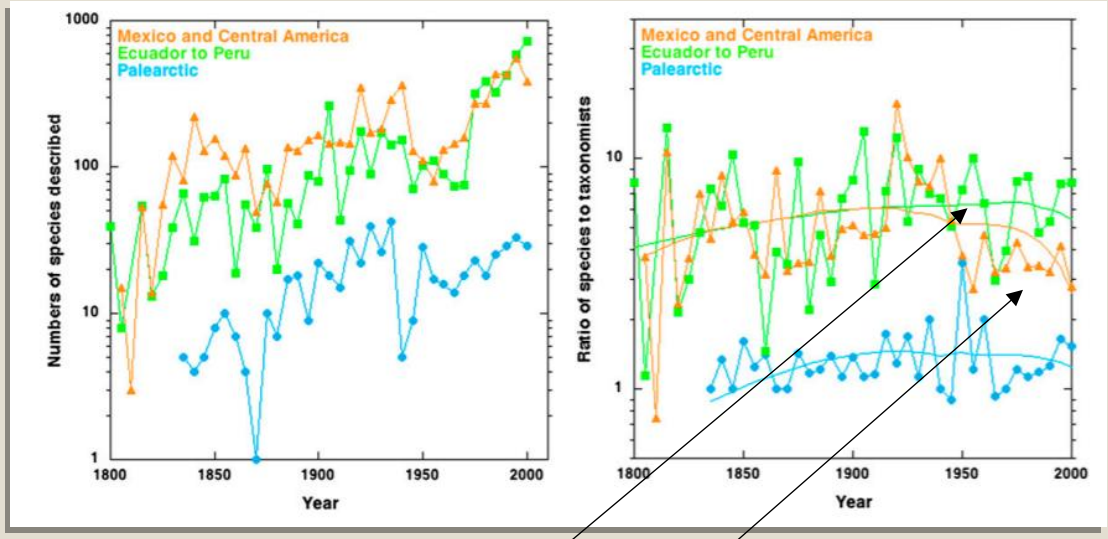
Samantha Caroniti

Introduction

- Known number of flowering plants form the basis of biodiversity hotspots
  - Hotspots are places where high levels of endemism (exist only in one geographic region) and habitat loss coincide to produce high extinction rate
  - < 30% of habitat remaining and numbers of endemic flowering plant species (>1500).
- 15% of flowering plant species are missing
- Questions to be discovered:
  - 1) Will knowing where there missing species reside change the way we set conservation priorities?
  - 2) Will relative priorities change as the taxonomic catalog gets completed?
  - 3) Will there be new priorities?
  - 4) Are the missing species in places where they are likely to be threated and will they be discovered before they become extinct?

Estimating missing species

- Two major problems:
  - 1. Taxonomists unintentionally give different names to the same species
  - 2. Rate of species descriptions
    - Expectation- numbers of new species per time interval decrease as unknown species decreases
      - Reality- exponential increase due to increase in number of taxonomists
    - Corrected numbers increased initially due to increasing taxonomic efficiency involving factors such as:
      - 1) better access to remote places, 2) increasing access to the literature and specimen in herbaria, 3) easier circumscription of taxa resulting from increasing number of species to compare.
      - Linearly increase over time.



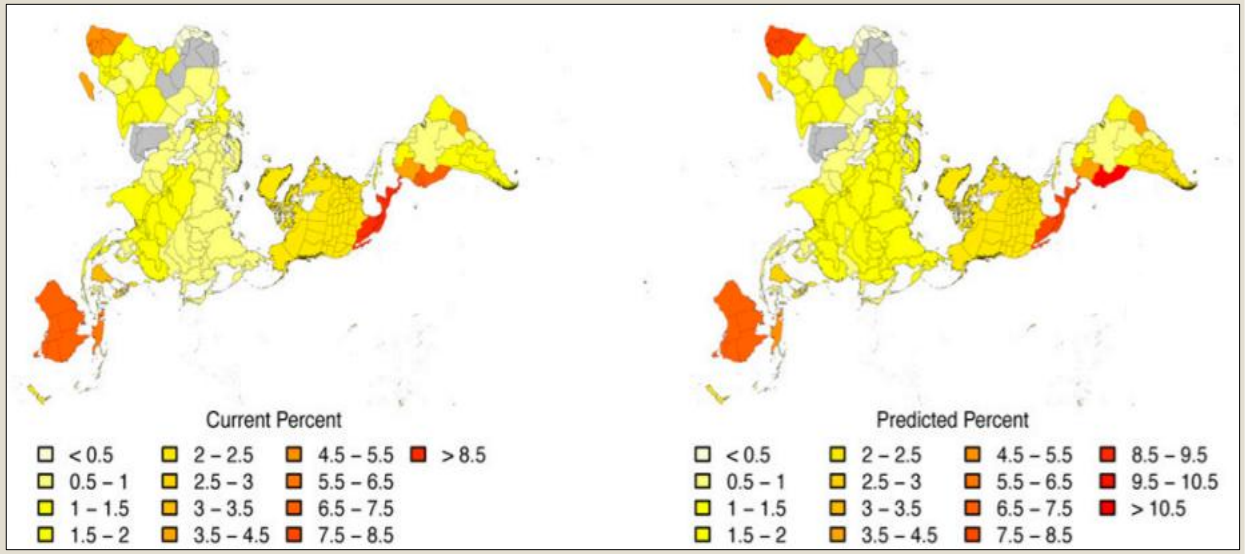
Graph explanation

- Decrease in the rate of sp. described per taxonomists
  - Increase that averages 15% more sp. than at present
- Ecuador-Peru & Palearactic
  - No decrease – missing sp.
- Plotted data start when region accumulated >40 endemic sp.

Results

- 79,000/108,000+ sp. were classified into one of the 50 regions (remainder occurring in two+ regions)
  - 21% predicted to be missing
- 40/50 regions show reduction over time in the number of sp. described per taxonomist per 5yr interval – leading to low ratios *(table, slide 5)*
  - More sp. Being discovered
  - Ex: Mexico and Central America- ratio is 1.17 *(table)* meaning an additional 17% will be predicted. We saw this on the graph from slide 5.
    - Same scenario for other hotspots with well-known flora such as Cuba, SE Brazil, & mainland tropical Asia.
- There is a rank change
- Existing conservation priorities would not be changed significantly by correcting the missing sp. *(slide 5)*
- Ecuador is ranked #2 & houses >5% of sp. In this sample
  - projected to contain 29% of the worlds missing species- this can be expected to overtake Mexico-Panama (#1)

Region	total, %	total, %	Ratio	species, %	change
North and Central America, Caribbean					
North America	2.47	2.10	1.09	0.77	↓ 1
Cuba	1.53	1.20	1.00	0.02	↓ 5
Caribbean islands other than Cuba	1.90	1.74	1.17	1.14	↓ 2
Mexico to Panama	9.00	8.24	1.17	5.50	↓ 1
South America					
Colombia*	3.62	4.15	1.46	6.05	↑ 2
Venezuela	1.90	1.78	1.20	1.33	→ 0
Guyanas	0.57	0.52	1.18	0.36	→ 0
Ecuador to Peru*	7.22	11.94	2.11	28.92	↑ 1
Bolivia	1.26	1.19	1.21	0.94	→ 0
Brazil, north	0.94	0.85	1.16	0.54	↓ 2
Brazil, northeast*	1.29	1.65	1.63	2.94	↑ 6
Brazil, south	0.72	0.62	1.10	0.25	→ 0
Brazil, west-central	0.72	0.65	1.15	0.39	↑ 2
Brazil, southeast	4.42	3.61	1.04	0.68	↓ 1
Paraguay, Argentina, Uruguay, Chile*	1.69	2.50	1.89	5.40	↑ 7
Temperate Eurasia					
Palearctic: Iceland to Western Siberia, south to Mongolia*	0.81	1.09	1.72	2.11	↑ 10
European Mediterranean	1.60	1.59	1.27	1.56	→ 0
North Africa and Middle East Mediterranean	0.89	0.90	1.29	0.92	↑ 1
Turkey	0.82	0.74	1.15	0.44	↓ 2
Caucasus	0.34	0.30	1.13	0.16	→ 0
Iraq, Iran, Afghanistan, Pakistan	0.73	0.66	1.15	0.41	↑ 1
Turkmenistan and Kazakhstan east through Tibet to Xinjiang, China	1.16	1.05	1.16	0.68	→ 0
China, south-central	1.94	1.98	1.30	2.13	↓ 1
China, southeast	1.50	1.47	1.25	1.37	→ 0
North-central China, Japan, Korea	0.77	0.65	1.08	0.21	↓ 2
Africa					
North East (Burundi, Ruanda, Uganda, Kenya, Somalia, Ethiopia, Eritrea, Sudan, Djibouti)	1.21	1.13	1.19	0.83	↑ 2
West Africa: Senegal to Benin*	0.46	0.47	1.31	0.52	→ 0
West and Central Africa: Nigeria to Central African Republic and Congo	1.27	1.08	1.08	0.37	↓ 6
Democratic Republic of Congo	0.73	0.67	1.18	0.47	↑ 4
Tanzania*	0.79	1.08	1.76	2.14	↑ 11
Angola, Malawi, Mozambique, Zambia, Zimbabwe*	1.16	1.25	1.37	1.55	↑ 7
Botswana and Namibia southward*	5.47	7.76	1.81	15.96	↑ 2
Madagascar	4.21	3.39	1.03	0.45	↓ 1
Tropical Mainland Asia					
Assam, Bangladesh, Himalayas, Burma, Nepal	1.46	1.26	1.11	0.55	→ 0
Indian, Sri Lanka	1.84	1.51	1.05	0.31	↓ 3
Thailand	0.96	0.78	1.03	0.12	↓ 5
Mainland Malaya	1.23	0.99	1.02	0.10	↓ 5
Cambodia, Laos	0.39	0.33	1.07	0.10	→ 0
Vietnam	1.15	1.11	1.24	0.98	↑ 5
Tropical Asia Islands					
Sumatra	1.25	0.98	1.00	0.00	↓ 7
Java, lesser Sundas	1.21	0.96	1.01	0.03	↓ 5
Borneo	3.30	2.65	1.03	0.31	→ 0
Sulawesi	0.74	0.61	1.05	0.14	↓ 4
Bismarck, Caroline, Marianas, Solomon Islands	0.80	0.67	1.06	0.18	↓ 2
Philippines	2.79	2.18	1.00	0.00	↓ 1
New Caledonia	1.50	1.29	1.10	0.52	→ 0
Fiji, Samoa, Society Islands, Tonga, Vanuatu	0.96	0.87	1.16	0.57	↓ 2
Australasia					
Australia*	7.09	7.29	1.31	8.02	↓ 1
New Guinea	5.74	4.52	1.01	0.14	↓ 1
Miscellaneous oceanic islands, worldwide	2.45	2.00	1.05	0.40	↓ 1
Total	100.00	100.00	—	100.00	—
Sample size	78,799	100,719	—	21,920	—
Species occurring across multiple regions	29,917	30,784	1.03	867	NA



*Current= currently known sp. from a sample of taxonomically revised families of flowering plants
Predicted= predictions of fractions once missing sp. are included
Ratio= predicted to currently known sp.
High ratio- >30% of sp. remaining to be discovered

Discussion: sources of uncertainty

- Total numbers of missing species in the 10 regions with the largest percentage of missing species are uncertain
  - Ex: Palearctic & Ecuador-Peru (map, slide 5)
    - Numbers of species describe are increasing and there is only a slight decline in the numbers of sp. described by taxonomists
- The rate limiting factor in the model might be the number of taxonomists available to describe the missing species, not necessarily the number of missing species
  - Difficult to find some missing flowers- size, location, hard to identify

Discussion: conservation priorities

- Great majority of the endemic missing species to be in hotspot regions
  - habitat loss is extensive: Mexico to Panama (6% of all predicted missing species), Colombia (6%), Ecuador to Peru (29%), Paraguay and Chile, southward (5%), southern Africa (16%), and Australia (8%)
  - Combined, contain 70% of all the species they predict to be missing—and these are not all of the hotspots.

ORCHID HISTORICAL BIOGEOGRAPHY, DIVERSIFICATION, ANTARCTICA AND THE PARADOX OF ORCHID DISPERSAL

Introduction

- Orchidaceae is the most species-rich angiosperm family
  - 8% of all vascular plants (880 genera and 27,800 sp.)
  - Broadest distributions
    - 72°N in Canadian Arctic Archipelago to 55°S in Tierra del Fuego
  - Grow in all terrestrial habitats (except driest deserts), native to all continents (except Antarctica)

Introduction (cont.)

- Drivers of diversity
  - Evolution of pollinia
  - Epiphytic habitat
  - CAM photosynthesis
  - Pollination via Lepidoptera, euglossine bee, and deceit
  - Life in extensive tropical cordilleras (Andes & New Guinea Highlands)
- Defining Characteristics
  - Minute seeds
  - Germination aided by fungal symbionts
  - Floral column of fused male and female parts

Questions and goals

- Questions blocked by lack of well-resolved, supported backbone phylogeny
  - Where did orchids originate?
  - To what extent do relationships above the generic level reflect intercontinental dispersal or vicarience event?
  - Does the diversity of orchids reflect their ability to disperse among continents, or is that limited?
  - Where did the key plant traits tht appear to have accelerated net rates of orchid diversification arise?
- Goal: Use a phylogeny to-
  1. Estimate the geographical spread of orchids
  2. Evaluate the importance of different regions in their diversification
  3. Assess the role of long distance dispersal (LDD) in generating orchid diversity

Paradox of orchid dispersal

1. The broad distribution and great diversity of orchids might reflect their dispersal by the dust like seeds of almost all sp.
2. Frequent long distance seed dispersal should work against differentiation within sp. and as a result, speciation.

- Suggested that only 34 orchid genera had been able to cross tropical oceans and establish distributions on continents that are long isolated from each other
  - S. America, Africa, SE Asia
  - Separation is seen within genera or closely related genera in orchid subfamilies
    - Except Apostasiodideae- may not have arisen early enough for continental drift to affect distribution
  - Only 3 sp. reached Hawaiian Islands
    - Limits imposed by: seed dispersal, or by missing pollinators or fungal symbionts

Methods

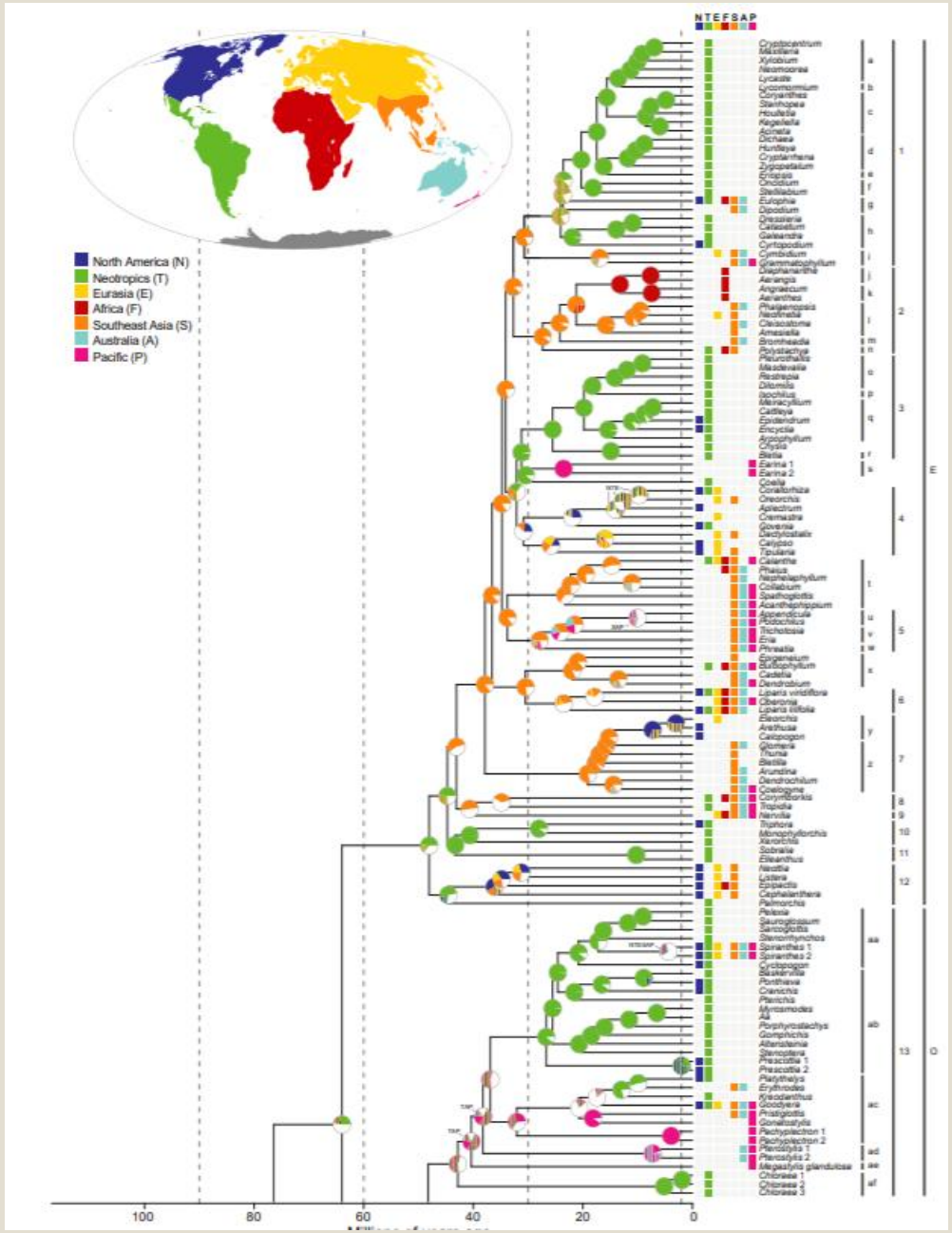
- Phylogeny including sp. representing 5 orchid subfamilies & almost all tribes/subtribes, calibrated against 17 angiosperm fossils
  - Use of the tree: Estimated historical biogeography, identify origin, assess roles of vicarience and intercontinental dispersal, and locate origin of epiphytism
    - Sequences of 75 plastid genes for 39 orchid sp. and 96 angiosperm outgroups, and 3 plastid genes of another 162 orchid sp.
- Historical biogeography
  - Max likelihood approach to estimate ancestral areas
  - Coded as present/absent for the 7 continents
  - Cypripedioideae and Vanilloideae represent lineages from different regions
  - Iridaceae and astelid families represent ancestral-area estimations
  - Dispersal probabilities among regions constrained based on emergent areas
    - Australia, S. Am, and Antarctica
      - Long distance dispersal, short distance dispersal (SE Asia & Wallace’s line), simple geographical spread with contiguous regions at dispersal time (SE Asia & Eurasia, N. Am & Neotropics)
      - Distributions were considered a result of vicarience (separation) if ancestors spread across formerly contiguous regions and then became extinct (Antarctica)

Methods (cont.)

- Assessed importance of different regions for rates of speciation, extinction, and net species diversification
  - For each region, an unconstrained model for diversification was compared to models where speciation, extinction, and character-state transition rates were individually constrained
    - Likelihood of constrained were compared to unconstrained, and significance of likelihood scores were assessed using ANOVA
    - Net rate diversification was calculated as speciation-extinction
- Evaluated the impact of particular LDD events on orchid diversity
  - Asked how many sp. evolved in the new range subsequent to those events
  - Calculated number of species resulting from each of the selected LDD events across tropical ocean
    - Based on position of events in pruned chronogram(records time) and number of sp. found per region
  - Studied all LDD events, LDD event preceding rise of the upper epidendroids, and LDD events preceding the origins of the pleurothallid alliance

Results

- Orchids appear to have arisen in Australia 112 Ma
- Spread to Neotropics via Antarctica by 90 Ma
  - When all 3 continents were in contact and apostasiods split from the ancestor of all other orchids
  - Origination of Vanilloids, cypripedioids, and orchidoids+epidendroids in 84-64 Ma
- Repeated long and short distance dispersal occurred through orchid history
  - Mean total of 74 LLD events found with stochastic mapping
- SE Asia was the most important source and maximally accelerated net diversification
  - Across epidendroids, the Neotropics maximally accelerated diversification
  - Presence in SE Asia led to highest advantage in net sp. Diversification (lower speciation and extinction rates)



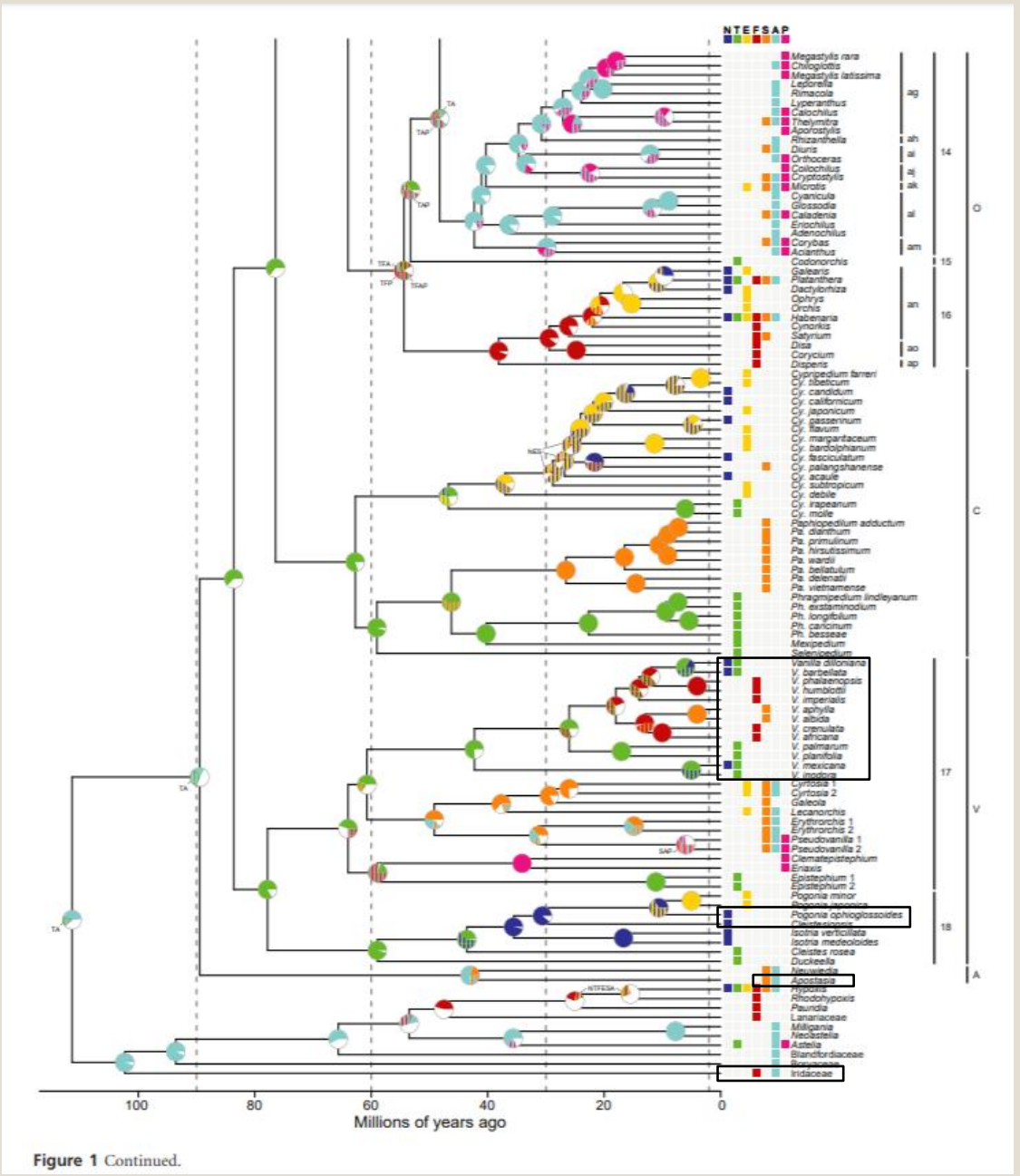


Figure 1 Continued.

Discussion/Conclusion

- First biogeographical history of orchids
- Origins are Australia, the Neotropics, and Antarctica
- LDD and life in Neotropics (Andes) had profound effects on their spread and diversification
  - >97% of orchid species are restricted to individual continents

Relation of both papers

- First paper: biodiversity hotspots
- Second paper: orchid history and dispersal

- Many species of orchids have high levels of endemism in the tropics, especially in the Andes

Samantha Caroniti

Biodiversity Hotspots House Most Undiscovered Plant Species (1)

For most organisms the number of described species underestimates how many are actually in existence- these unknown species are called "missing" species. This is a big problem and causes complications given present high rates of species extinction. The known number of flowering plants, which is what I will focus on today, forms the basis of biodiversity "hotspots." **Hotspots** are places where high levels of endemism and habitat loss coincide to produce high extinction rates- as a reminder endemism means that a species exists in one geographic region. A more clear description of a hotspot would be that they are geographical concentrations of threatened species caused by habitat destruction (<30% of the habitat remaining) and numbers of endemic flowering plant species (>1500). These hotspots are priorities for conservation. There are some questions that need to be considered: 1) with the taxonomic catalog being incomplete, are there additional areas that should be considered hotspots if we knew more about the number of species within them? 2) If we had complete information, would the rankings of the hotspot change?

Next slide (2)

It is estimated that we only know 85% of flowering plant species, meaning that 15% are still missing. It was/is assumed that some of the species might be locally rare and geographically restricted and a rare exception that many have been collected are waiting in herbaria to obtain a taxonomical description. There are more questions that authors of this paper wanted to discover: 1) Will knowing where there missing species reside change the way we set conservation priorities? 2) Will relative priorities change as the taxonomic catalog gets completed? 3) Will there be new priorities? 4) Are the missing species in places where they are likely to be threated and will they be discovered before they become extinct?

Next Slide (3)

There are two major problems that are encountered when estimating the number of missing species:

1) Taxonomists unintentionally give different names to the same species
    a. This issue is avoided by using the World checklist of Selected Plant Families that includes the location of the species. However the taxonomy has only been reviewed for some families- all monocots (60,000 sp. excluding grasses- different database w/out location (TDWG) - not included in analysis) and 50,000 monocots.
2) Involves the rate of species descriptions
    a. Earlier studies attempted extrapolate the number of species over time, with the expectation that the numbers of new species per time interval will decrease as unknown species decreases. In reality, the rates showed an exponential increase- this was due to the increase in number of taxonomists (part of the formula they use to estimate number of sp. remaining to be described). In the past century, number of species described dived by taxonomists involved has decreased. The data is corrected for the number of taxonomists involved in the description of the sp., and it usually shows an increase initially, as seen in figure 1 (rt), this due to increasing taxonomic efficiency involving factors such as 1) better access to remote places, 2) increasing access to the literature and specimen in herbaria, 3) easier circumscription of taxa resulting from increasing number of species to compare. This should increase linearly over time. On the right side

of the graph, in the most recent years, there eventually is a decrease in the rate of sp. described per taxonomist leading to an increase that averages 15% more species than at present. This example is demonstrating the change in Mexico and Central America. Where there is no decrease, in Ecuador-Peru and Palearctic, this suggests that that a number of species are still missing.

Next slide (4)

From their sample of 108,000 species, they predict 21% of species are missing. This is similar to the estimates made for the monocots (17%) and nonmonocots (13%) as I mentioned earlier. 40 out of the 50 regions show reduction over time in the number of sp. described per taxonomist per 5yr interval – leading to low ratios (more sp. Being discovered). An example would be Mexico and Central America- on the table the ratio is 1.17 meaning an additional 17% will be predicted. We saw this on the graph from **slide 3**. The same goes for other hotspots with well-known flora such as Cuba, SE Brazil, & mainland tropical Asia.

To answer Q1, yes. There is rank change as we see in the table on **slide 6**. Also on slide 6, there is a map of currently known patterns of flowering plant species richness and the patterns when corrected for species predicted to be missing from the taxonomic record. The similarities between these two maps along with the table indicate that existing conservation priorities would not be changed significantly by correcting the missing sp. For example- forests of South America will remain major centers of plant endemism as well as areas under threat. That being said, there are geographic differences between the known and predicted. In this sample, Ecuador and Peru house more than 5% of the species and is ranked 2nd as the richest area. The region, however, is projected to contain 29% of the worlds missing species- this can be expected to overtake Mexico-Panama (#1).

Next slide (5)

Table & map

Next slide (6)

There are a few sources of uncertainty. First, the total numbers of missing species in the 10 regions with the largest percentage of missing species are uncertain- the map on slide 7 shows the Palearctic and Ecuador/Peru. Numbers of species describe are increasing and there is only a slight decline in the numbers of sp. described by taxonomists. The second source of uncertainty is that the rate limiting factor in the model might be the number of taxonomists available to describe the missing species, not necessarily the number of missing species. It is hard to find some of the missing flowering plants such as orchids, as they might be very small in size and if found or in a location that can't be accessed, they might be hard to identify.

Next slide (7)

To conclude, it is predicted that the great majority of the endemic missing species to be in hotspot regions where, by definition, habitat loss is extensive: Mexico to Panama (6% of all predicted missing species), Colombia (6%), Ecuador to Peru (29%), Paraguay and Chile, southward (5%), southern Africa (16%), and Australia (8%) combined have 70% of all the species they predict to be missing—and these are not all of the hotspots.

Orchid Historical Biogeography, Diversification, Antarctica and the Paradox of Orchid Dispersal

Next slide (9)

Orchidaceae is the most species rich angiosperm family with 880 genera and 27,800 species. They make up 8% of all vascular plants and grow in almost all terrestrial habitats except for the driest deserts and are native to all continents except Antarctica. They also have the widest latitudinal range of any plant family starting from the Canadian Arctic Archipelago to Tierra del Fuego in S. Am.

Next slide (10)

The drivers of diversity include Evolution of pollinia; Epiphytic habitat; CAM photosynthesis; Pollination via Lepidoptera, euglossine bee, and deceit; and Life in extensive tropical cordilleras (Andes & New Guinea Highlands). You could define an orchid by Minute seeds, Germination aided by fungal symbionts, and Floral column of fused male and female parts

Next Slide (11)

This paper makes note of questions that were not able to be answered due to the lack of a well resolved phylogeny of the orchids: Where did the orchids originate? To what extent do relationships above the generic level reflect intercontinental dispersal or vicariance events? Does the remarkable diversity of orchids reflect their ability to disperse among continents, or is that ability limited? Where did the key plant traits that appear to have accelerated net rates of orchid diversification arise? A phylogeny was derived and the goal was to use it to Estimate the geographical spread of orchids, Evaluate the importance of different regions in their diversification, and to Assess the role of long distance dispersal (LDD) in generating orchid diversity.

Next slide (12)

It seems reasonable that high orchid diversity may reflect their broad distribution which raises the term of “Paradox of orchid dispersal.” There’s the idea that the broad distribution of orchids might reflect their excellent dispersal conferred by the dust like seeds of almost all species, and on the other hand, frequent long distance dispersal (LDD) should work against differentiation within species and as a result, speciation. It was suggested that only 34 orchid genera had been able to cross tropical oceans and establish distributions on continents that are long isolated from each other, such as S. America, Africa, SE Asia. These disjunctions are seen within genera or closely related genera in orchid subfamilies except Apostasiodideae- as they may not have arisen early enough for continental drift to affect distribution. Also, only 3 sp. reached Hawaiian Islands, with suggestions that the limits were imposed by: seed dispersal, or by missing pollinators or fungal symbionts.

Next slide (13)

The analyses use a phylogeny including sp. representing 5 orchid subfamilies & almost all tribes/subtribes, calibrated against 17 angiosperm fossils. This tree allowed for the researchers to estimate historical biogeography, identify origin, assess roles of vicarience and intercontinental dispersal, and locate origin of epiphytism. The tree is based on sequences of 75 plastid genes for 39 orchid sp. and 96 angiosperm outgroups, and 3 plastid genes of another 162 orchid sp. First, we look at historical biogeography. The researchers used the max likelihood approach to estimate ancestral areas and coded the species as present/absent for the 7 continents. On the tree we will see certain representatives-

Representatives of the individual genera were coded based on the entire distribution of that genus except for the species of Cypripedioideae and Vanilloideae; they represent lineages from different regions. Iridaceae and astelid families act as representatives for ancestral-area estimations. Dispersal probabilities among regions were constrained based on their emergent areas. For example, the dispersal between Australia and S. Am take into account their previous connection with Antarctica. Movement between the regions were considered to be Long distance dispersal, short distance dispersal (across short distances of water that separate SE Asia & Australia at Wallace's line), and simple geographical spread with contiguous regions at dispersal time (SE Asia & Eurasia, N. Am & Neotropics). Distributions were considered a result of vicarience (separation) if ancestors spread across formerly contiguous regions and then became extinct (such as Antarctica)

Next slide (14)

As another method, they assessed importance of different regions for rates of speciation, extinction, and net species diversification. For each region, an unconstrained model for diversification was compared to models where speciation, extinction, and character-state transition rates were individually constrained. The likelihood of constrained were compared to unconstrained, and the significance of likelihood scores were assessed using ANOVA. The net rates of diversification were calculated as speciation minus extinction. As mentioned before, they also evaluated the impact of particular LDD events on orchid diversity. The numbers of species resulting from each of the selected LDD events across tropical ocean were calculated based on position of events in pruned chronogram(records time) and number of sp. found per region. They studied all LDD events, LDD event preceding rise of the upper epidendroids, and LDD events preceding the origins of the pleurothallid alliance.

Next slide (15)

Moving on to the results, the model shows that Orchids appear to have arisen in Australia 112 Ma when Australia and S. Am were connected with Antarctica, and then spread to Neotropics via Antarctica by 90 Ma; so when all 3 continents were in contact, apostasiods split from all other orchids and reached SE Asia during the last 43 Ma. Ancestors of Vanilloids, cypripedioids, and orchidoids+epidendroids appeared to originate in the Neotropics 84-64 Ma. They repeated long and short distance dispersal occurred through orchid history such as within Vanilloids and so on. A mean total of 74 LLD events were found with stochastic mapping. SE Asia was the most important source and maximally accelerated net diversification because of lower speciation and extinction rates. Across epidendroids, the Neotropics maximally accelerated diversification compared to other regions.

Next slide (16)

This was the diagram depicting estimation or orchid historical biogeography. Pie diagrams at each node represent regions inferred to have been occupied by ancestral taxa. Wedge color indicates ancestral region. Distributions of the genera and individual sp. are indicated by colored boxes. The vertical lines indicate subtribes, tribes, and subfamilies.

Next slide (17)

To conclude, this was the first biogeographical history of orchids to be created. The origins of orchids are Australia, the Neotropics, and Antarctica. And LDD and life in Neotropics (Andes) had profound effects on their spread and diversification- >97% of orchid species are restricted to individual continents.