IB 168 -- Key Concepts: PLANT GEOGRAPHY Spring 2009

Plant geography is concerned with the distribution of plants in space and time.

Historically, plant geographers with an <u>ecological</u> focus have tended to concentrate on <u>vegetation</u>; those with an evolutionary or <u>systematic</u> focus have concentrated on <u>flora</u>.

VEGETATION: Organization of communities and associations of plants, often looking for ecological properties that transcend the taxa involved. For example, a biogeographer concerned with vegetation may compare chaparral scrub communities in different parts of world, where the species involved are completely different but the structure and functioning of the communities may be similar.

FLORA: The species (lineage) composition of plants of a particular region, i.e., the actual taxa found within a region; not directly concerned with interactions between species.

Documentation of the floristic composition of different regions led to recognition of floristic areas, sometimes treated within a hierarchy of floristic kingdoms, regions, and provinces.

FLORISTIC AREAS: areas of distinctive flora, with relatively uniform floristic composition (e.g., California Floristic Province – an area of Mediterranean Climate). Floristic areas often map onto areas of distinctive climate and animal composition that correspond to general biotic regions. Floristic areas are diagnosed in part by <u>endemics</u>.

ENDEMISM: Restriction of plants to a particular area or setting (e.g., restriction to unusual soils = edaphic endemism). Plants restricted to an area are considered *endemic* to that region.

Two general classes of endemics are widely recognized:

PALEOENDEMICS ("ancient endemics") = relicts = organisms (in our case, plants) that are restricted to an area because they have died out elsewhere. A fossil record elsewhere is the best evidence for paleoendemism (e.g., in *Sequoia*, *Sequoiadendron*, *Lyonothamnus*). The current range of paleoendemics is often referred to as the relictual distribution. Also, molecular data may indicate that paleoendemic lineages are more ancient than the unique environmental conditions in the region where they occur (another line of evidence for paleoendemic status).

NEOENDEMICS ("new endemics") = organisms (e.g., plants) that are restricted to an area because they evolved there. Phylogenetic data may indicate that neoendemic lineages constitute monophyletic groups of young age relative to the age of their habitat (e.g., island age) or the unique environmental conditions there, as expected.

OTHER USEFUL, GENERAL CONCEPTS IN PLANT GEOGRAPHY THAT APPLY TO TAXA OR LINEAGES:

Native or indigenous = naturally occurring in the area of concern; occurrence in that area is not a result of human activities or influences.

Exotic = not native or indigenous to an area.

Naturalized = Established and reproducing without human intervention, but occurring in the area of concern as a result of human activities or influences (not native). Naturalized taxa include those that enter an area without direct or intentional human aid but would not have reached the area without earlier activities by humans or their agents.

Extirpated = eliminated from the area of concern but surviving elsewhere.

Extinct = eliminated everywhere; surviving nowhere.

Extant = not extinct.

INTRODUCTION TO HISTORICAL BIOGEOGRAPHY (concerned with understanding how organisms attained their current, native distributions):

General (oversimplified) question in historical biogeography:
WHY NOT A UNIFORM FLORA WORLDWIDE?
One obvious reason: Abiotic and biotic environmental factors differ in different parts of the world; for example, climatic differences at different latitudes will cause plants with different physiological tolerances to sort out accordingly.

BUT:
(1) Why do different areas with seemingly identical conditions have different floras? For example, why should the Galapagos Islands of the Pacific Ocean have a different biota than the Cape Verde Islands of the Atlantic Ocean? This is a question asked by Darwin in his Origin of Species.

(2) The most frequently asked question in historical biogeography: Why do similar (closely-related) species have discontinuous (disjunct) distributions?

DISJUNCTIONS: Natural gaps in the geographic ranges of taxa; for example, between populations of the tarweed *Carlquistia muirii* in the southern Sierra Nevada and in the South Coast Ranges of California.

Causes of disjunctions:
a) **Chance Dispersal**: Movement of plants via long-distance transport of propagules (e.g., seeds, vegetative segments) from one area to another (mediated by physical or biological agents). In island archipelagos, long-distance dispersal of plants from one island to another is often referred to as "island hopping." In most cases, long-distance dispersal is probably an extremely rare event, carrying the plant far beyond its normal

dispersal range and greatly reducing the likelihood of gene flow with the ancestral population.
b) **Vicariance:** Break-up of once-continuous distributions by extirpation of plants in intervening areas or physical separation of the areas via geological processes (e.g., loss of a land bridge between two areas, mountain building or a new river course separating plants on either side, tectonic movement of land masses away from one another, etc.).

Following either vicariance or dispersal, evolutionary divergence of the disjunct populations or sets of populations may occur. Phylogenetic analyses may reveal the evolutionary relationships among the resultant lineages and allow for reconstruction of the events that resulted in their original separation from one another.

LONG-DISTANCE DISPERSAL: This possible explanation for disjunctions was recognized by early botanists; for example, the 18th Century botanist Linnaeus believed that all plants were originally created on a tropical island (the literal Garden of Eden), from which dispersal occurred and yielded modern distributions.

VICARIANCE: First suggested by 19th Century botanist Asa Gray (at Harvard University) for disjunctions between eastern North American and east Asian forest taxa. He believed that eastern North America and eastern Asia have too many closely-related species in common to imagine that these patterns arose by a whole series of separate long-distance dispersal events (too many accidental events in common). Instead, he hypothesized the break-up of a once continuous north temperate forest by climatic changes.

VICARIANCE was not widely appreciated until after documentation of **continental drift** in early 1960s (first proposed by Wegener in early 1910s) via **plate tectonics** (e.g., ocean floor spreading of mid-Atlantic ridge) and development of **phylogenetic methodology**.

Croizat (1950s and 60s) looked at sister-species distributions, connected them with lines and searched for common lines after examining many pairs of distantly related species. He referred to these biogeographic lines or connections across the globe as TRACKS. Although the causes of these tracks were not explored, Croizat's method of looking for common distributional patterns was widely cited by subsequent vicariance biogeographers.

Vicariance biogeography: Nelson, Platnick, and Rosen (1970s) combined phylogenetic methodology with "area relationships" to **test vicariance in explaining disjunct distributions**.
They pointed out that dispersal can't be tested; that is, that routes of dispersal are unpredictable (<u>but likely routes of dispersal can be tested in some cases, e.g., within hot-spot archipelagos such as the Hawaiian Islands, where the simplest hypothesis is that dispersal occurred from older to younger islands</u>).

PREDICTIONS UNDER VICARIANCE:

1) Sister-group relationships of groups found in different areas should reflect the pattern of break-up of those areas. For example, if different species are found in the South America, Africa, Madagascar, and India, then, based on what we know about the sequence of break-up of those areas via continental drift, (1) the South American species should be sister to the African species, (2) the Madagascar species should be sister to those from India, and (3) groups 1 and 2 should be sister to one another. If those relationships are not found, then dispersal must be invoked to account for discrepancies. That is, the relationships of taxa restricted to particular areas should match the "relationships" (sequence of break-up) of the areas, which can be expressed as an AREA CLADOGRAM.

2) If vicariance accounts for the disjunctions among a set of taxa, then the relationships of other groups of plants or animals that show the same geographic distributions should also fit the "area cladogram," unless dispersal has occurred. The finding of additional examples of conformance to the "area cladogram" strengthens the vicariance hypothesis.

3) Finally, a new consideration has come into play, based on the possibility now of acquiring dates for divergence events in molecular phylogenies: Not only does the PATTERN of relationships need to be considered but also the TIMING of divergence between sister groups. If the timing of divergence is much different than the timing of geological or climatic events that established the patterns in the area cladogram, then congruence of the species tree and area cladogram should not be expected.

PATTERNS OF RELATIONSHIP:

Under vicariant "speciation", sister-group relationships are expected between taxa. Traditional expectations under vicariance are that the sister-lineages will undergo gradual divergence in isolation and may become evolutionarily distinct (with or without significant or detectable changes in their ecological characteristics).

Under dispersal, the dispersed group is expected to be phylogenetically "nested" within the group from the ancestral area; that is, the group of taxa from the ancestral area will be paraphyletic relative to taxa in the new area (unless the dispersal event out of the ancestral area happens more rapidly than diversification there).

Taxa that manage to disperse to areas with many unoccupied niches (e.g., in oceanic islands) may undergo adaptive radiation, i.e., rapid diversification into different ecological forms, a possible outcome of major ecological opportunities ("ecological release") and absence of competitors ("competitive release"). In adaptive radiations, ecological factors rather than geographic isolation are the most important drivers of evolutionary divergence.