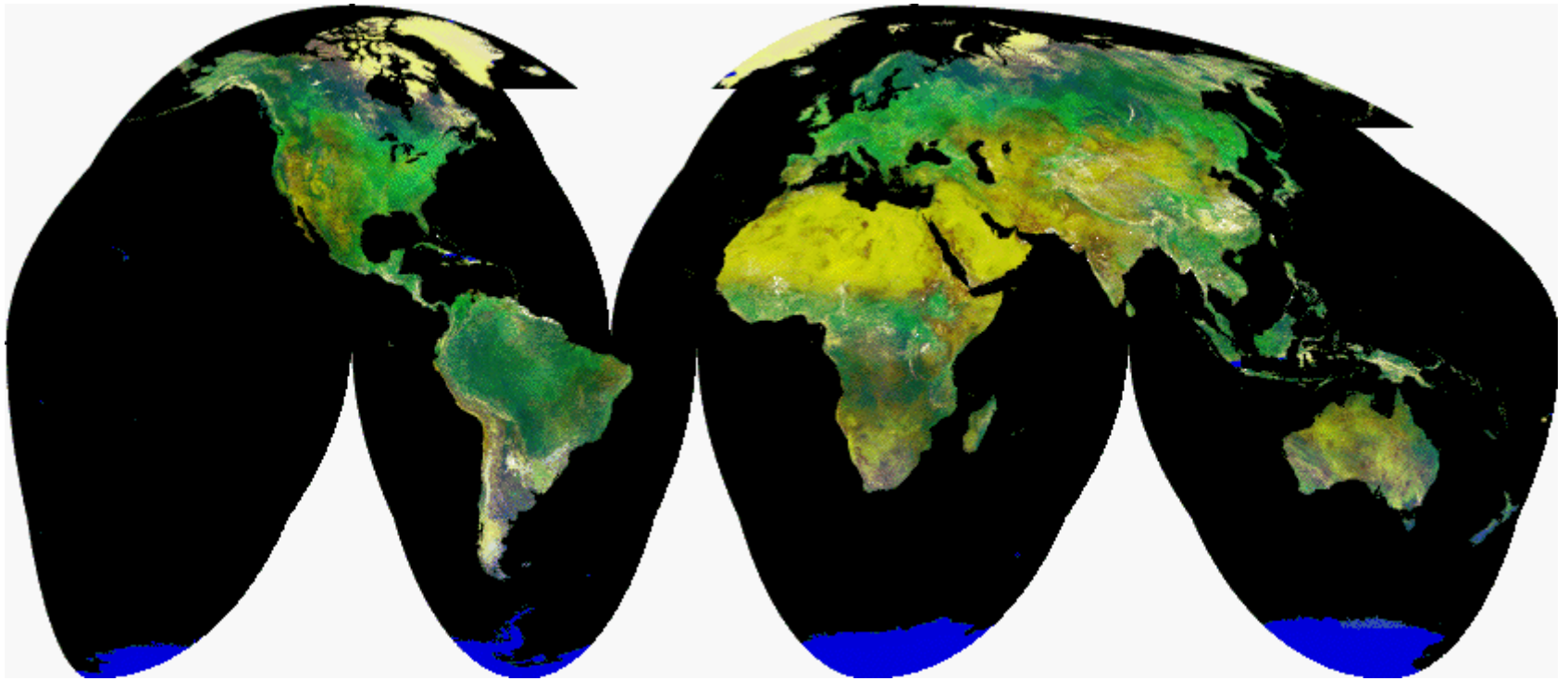


Introduction to Case Study Research Approaches: Biogeography



ISLAND BIOGEOGRAPHY

- Islands have had a significant impact on biogeography. Why?
- Islands and other isolated "island" habitats, such as mountaintops, springs, lakes and caves, are ideal for natural experiments
 - the islands are well defined
 - relatively simple
 - isolated
 - and numerous (there are tens or hundreds of islands in the archipelagos)

Islands as natural experiments

- As in the laboratory experiments, the islands vary in some environmental parameters, e.g.
 - area
 - degree of isolation
 - presence or absence of predators and competitors etc.
- Therefore, the effect of these factors on the bio-community of the island can be estimated

The theory of island biogeography

- The theory of MacArthur and Wilson (1963 and 1967) was developed to explain two general patterns in island biogeography:
 - the tendency for the number of species to increase as the island area increases
 - and to decrease as insular isolation increases

Biogeography

The relationship between area and number of species

- A regardless of taxonomic group or ecosystem under consideration, the number of species tends to increase as the area increases.
- But this increase is not linear, as the number of species increases less the larger the islands are.

Biogeography

The mathematical expression of the relationship

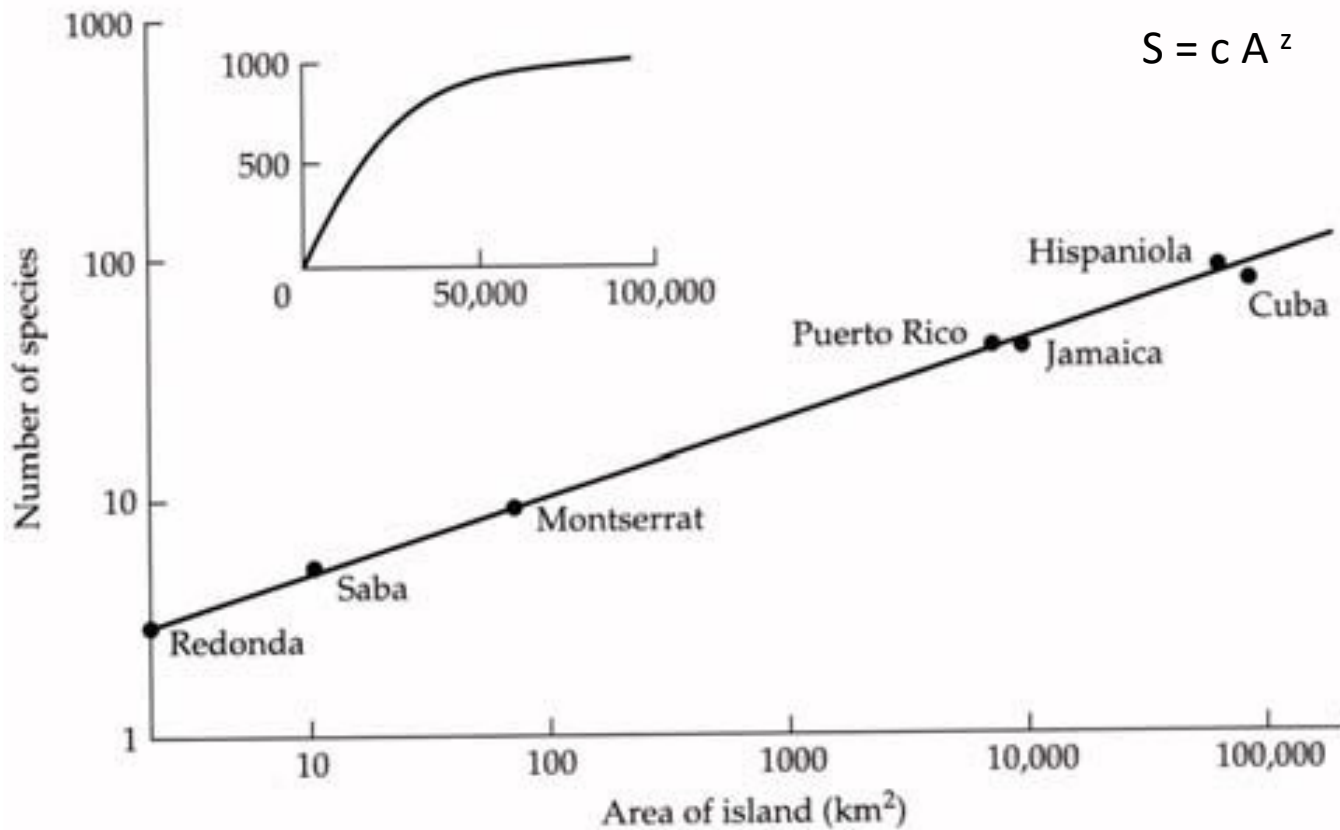
- Olof Arrhenius (1920) adapted the allometric equation to describe the relationship between number of species and habitat area. The equation he proposed was called **potential model** and is simply expressed as:

$$S = c A^z$$

- where S = the number (richness) of species, c = a constant, A = the area of the island, and z = another constant, representing the slope when S and A are plotted in logarithms scales. With logarithm, the relationship becomes linear:

$$\log(S) = \log(c) + z \log(A)$$

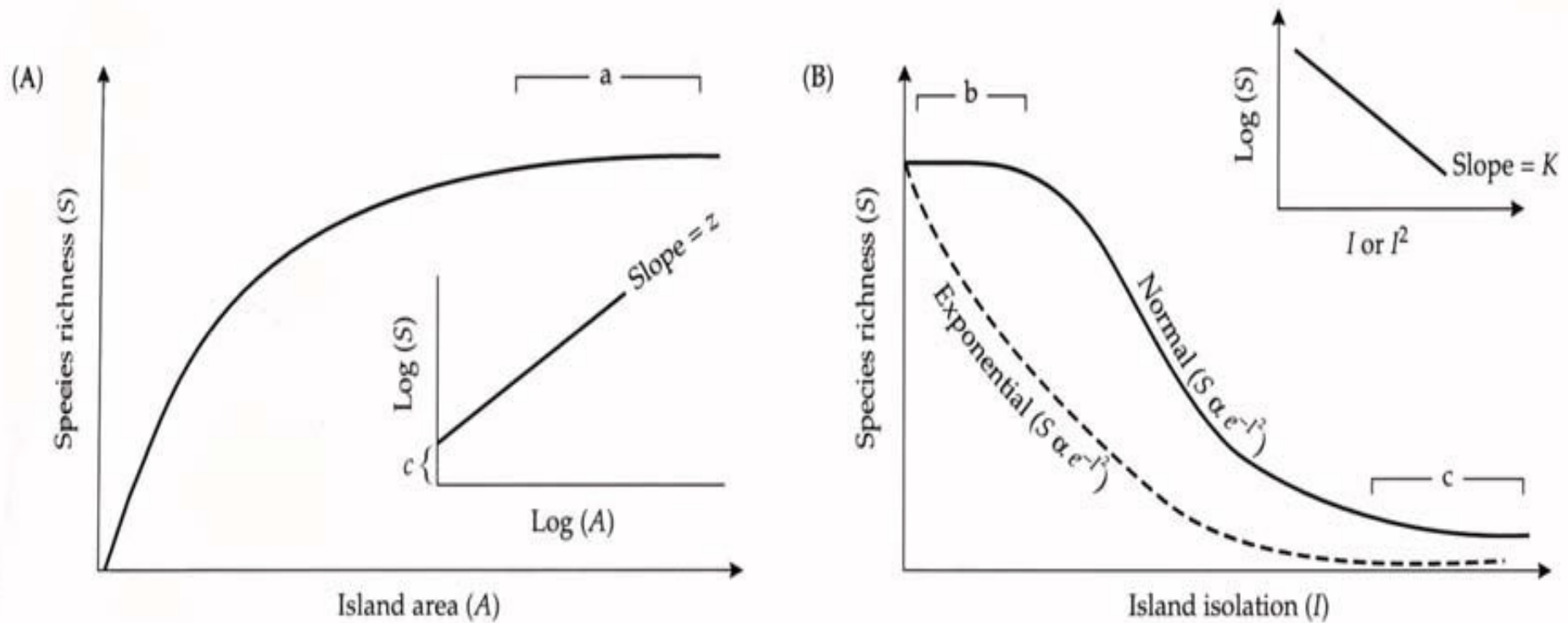
- The constants c and z can be easily determined by simple regression for logarithmic data.



The empirical relations between species richness (S) and island extent (A) for reptiles and amphibians in the West Indies (primary data from Darlington 1957). In the big diagram the two axes are in **logarithmic scale** and the relationship is expressed by a straight line. In the insert diagram the relationship is expressed in **arithmetic scale**.

The species-area relationship

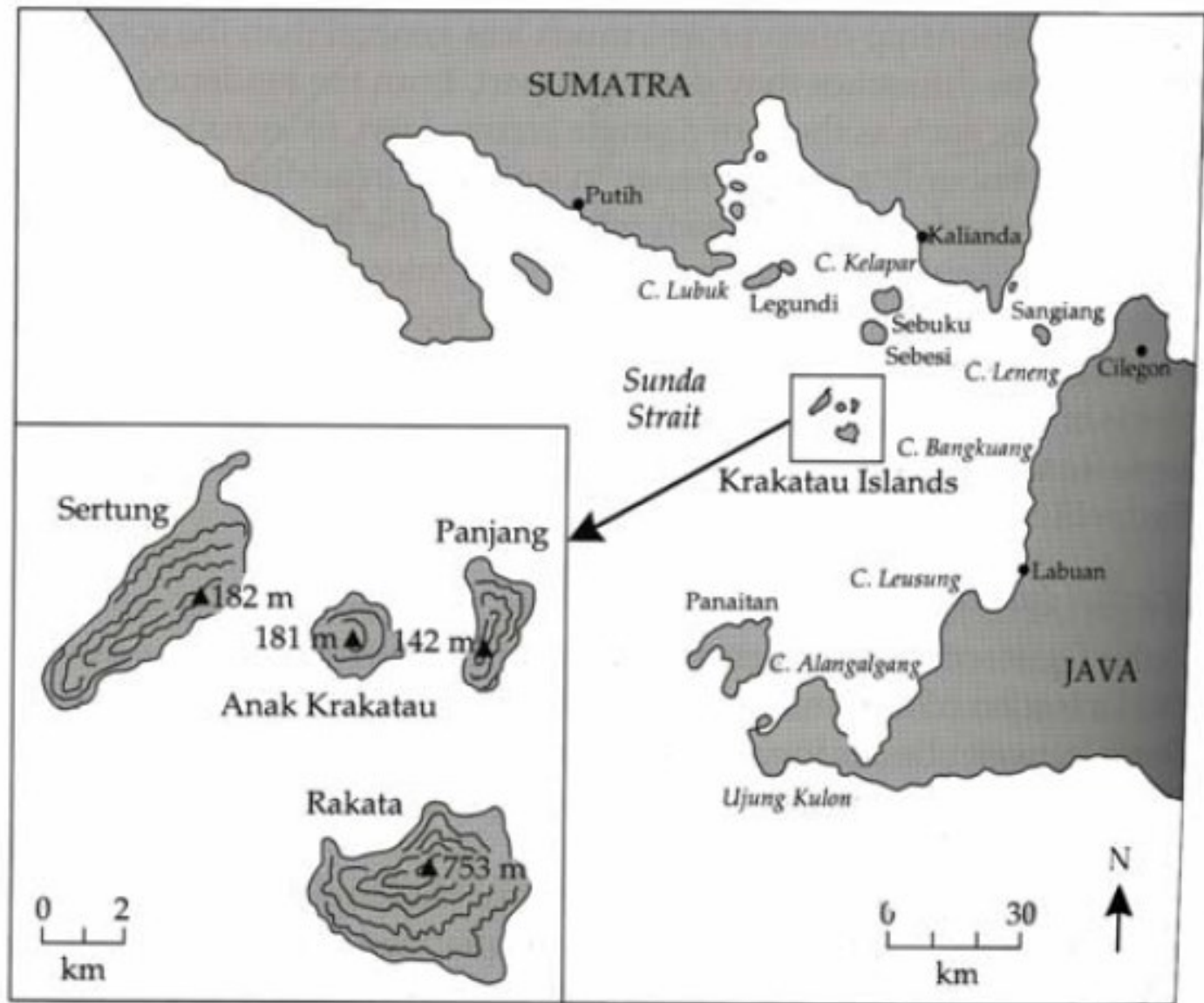
- Since the early 1800s it was known that **isolated and very remote islands support fewer species** than islands that form parts of archipelagos, or are located near continents.
- Considering that this is a **consequence of the great isolation** (with the increase of isolation **the dispersal rate decreases**), the form of the species-isolation relationship on the islands, is a consequence of a change (decrease) in the dispersal of the species **from the "source"** of mainland species.
- Therefore, for a variety of taxa and ecosystems, **species richness must decrease in relation to isolation**



Two of the most common patterns, in nature, of the relationships of (A) number of species and area and (B) number species and isolation. In the inset diagrams the same relationships on a logarithmic scale (S = number of species, A = area island, I = degree of island isolation, c and z = constants of the equation). On very large islands, where the slope is almost zero (area a in A), it is difficult to describe the relationships and thus a biogeographical study should not only include large islands. Similarly, the study of the species-isolation relationship should cover islands with a wide variation of isolation (to avoid only areas b and c in B).

Species Turnover

- A third pattern that influenced MacArthur and Wilson was the rapid re-colonization of the Krakatoa
- A volcanic eruption destroyed the original island Krakatau, in 1883, leaving several small islands without macroscopic life forms.
- The re-colonization by the neighboring large islands of Java and Sumatra was fast
- By 1935 (in 52 years) a tropical rain forest had developed that supported many species of plants, birds and other groups. These islands have since been regularly visited by scientists to study their species compositions.



The islands of Krakatau, between Sumatra and Java, destroyed by a volcanic eruption in 1883. In 1930, a new small island, Anak Krakatau, was formed by volcanic eruptions.

Biogeography

The islands of Krakatau

- MacArthur and Wilson observed that **the number of bird species** on the islands Rakata and Sertung increased rapidly until 1920 but, after that, the total number of species **remained relatively stable**, despite the changes in the composition of the avifauna.
- The colonisation continued after 1920 and some of these colonisers were successful and replaced an approximately equal number of extinct species.
- These equilibrating colonizations and extinctions may simply have reflected **successive changes** in the avifauna in response to the growth of a rainforest and subsequent restriction of open habitats.
- Possibly, however, this constant **replacement** to it is **typical of island communities** and becomes particularly large when organisms need it to cross only moderate barriers to reach the small islands

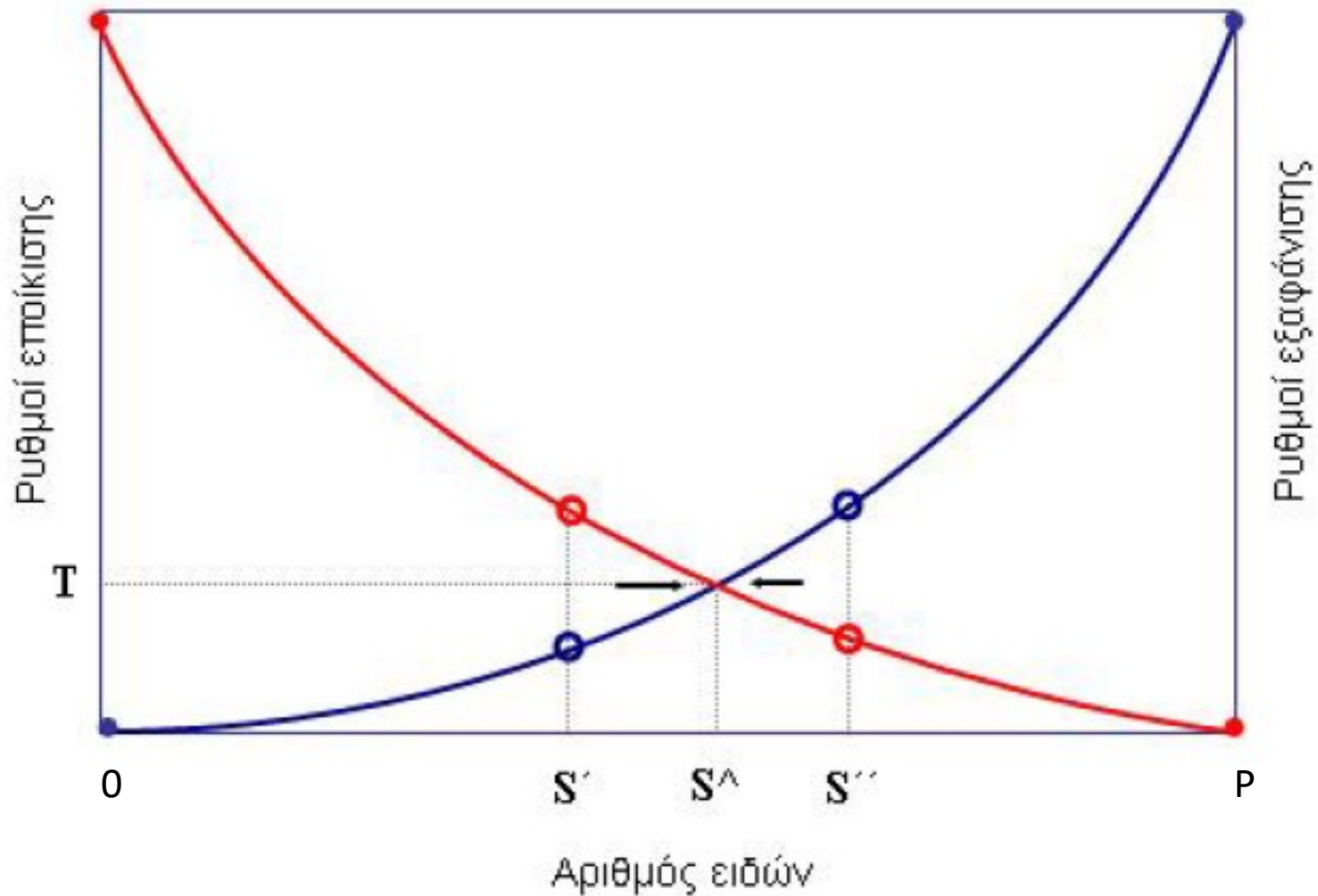
Biogeography

The equilibrium theory in island biogeography

- MacArthur and Wilson developed a unified theory to interpret the three main characteristics of island communities:
 - the area-number of species relationship
 - the isolation-number of species relationship
 - and species turnover

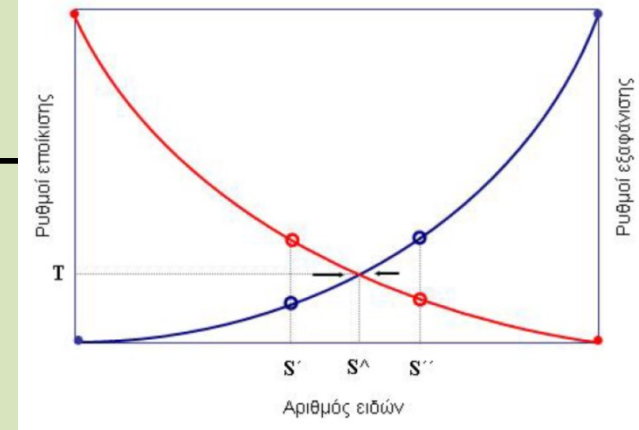
Biogeography

- They suggested that the number of species present on an island represents a dynamic balance between the (opposite) rates of **population** and **extinction**
- The balance it is labeled "dynamic" because settlement and extinction are considered to be **repeated**, continuous, opposite **processes**, contributing to the maintenance of a relatively constant number of species, despite changes in species composition.
- The equilibrium model **can be shown graphically by plotting the rates colonization and extinction** as a function of the number of species present on an island



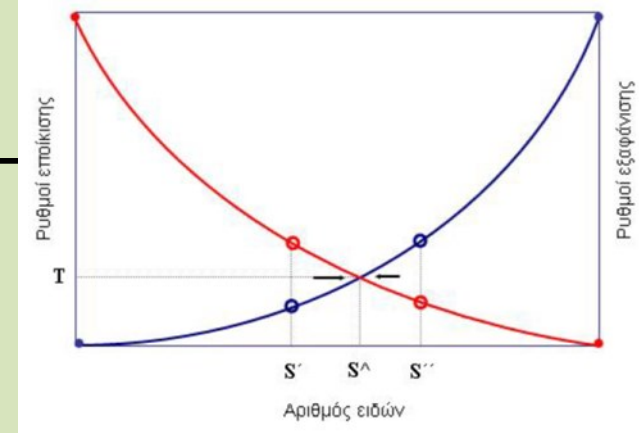
A simple model, according to which the number of species inhabiting an island is a function of the rates of two opposite processes: colonization and extinction. As the number of species varies from 0 to P (P is the number of "source" species that will potentially come to the island) the colonisation rates decrease and the extinction rates increase. The point of intersection of the two curves determines the number of species that the island can accommodate (S^A) and constitutes a point of balance, to which the island returns when, for any reason, its species richness changes (from S' or S'' value species richness will revert to the S^A value, according to the arrows).

Biogeography



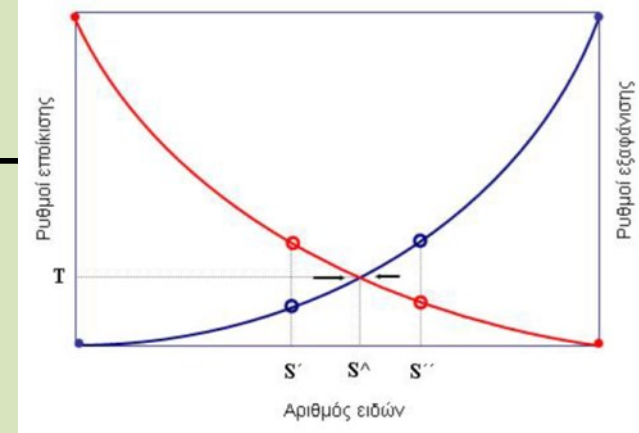
- The number of species on an island (S) can range from zero, when the island has no species, up to a maximum, P , when it carries as many species as those of the "source", that is, all species of a neighboring continental, or other, area that harbours potential colonisers.
- We can therefore predict the shape of the settlement curves and extinction.

Biogeography



- At some value of the number of species, between zero and P , the curves representing the rates of colonisation and extinction intersect.
- At this point the two rates are equal and then on the island there is a balanced number of species, S^\wedge , and a balanced rate of species turnover, T^\wedge .
- That is, this point shows the species richness that the island under consideration can support, and represents a **dynamic balance**.

Biogeography



- For example, if a natural disaster wiped out some species on an island and reduced their numbers from S^A to S' . Then, the colonisation rate will exceed the extinction rate and the island will again accumulate species until it reaches the value S^A .
- Likewise, if for some reason the introductions of new species increase and the species from S^A become S'' , then extinctions will increase over colonization until all species recover at point S^A .

Biogeography

Effect of island size and isolation on the model

- MacArthur and Wilson hypothesized that the size of the island affects the rate extinction.

And that

- colonisation rate is affected by isolation.

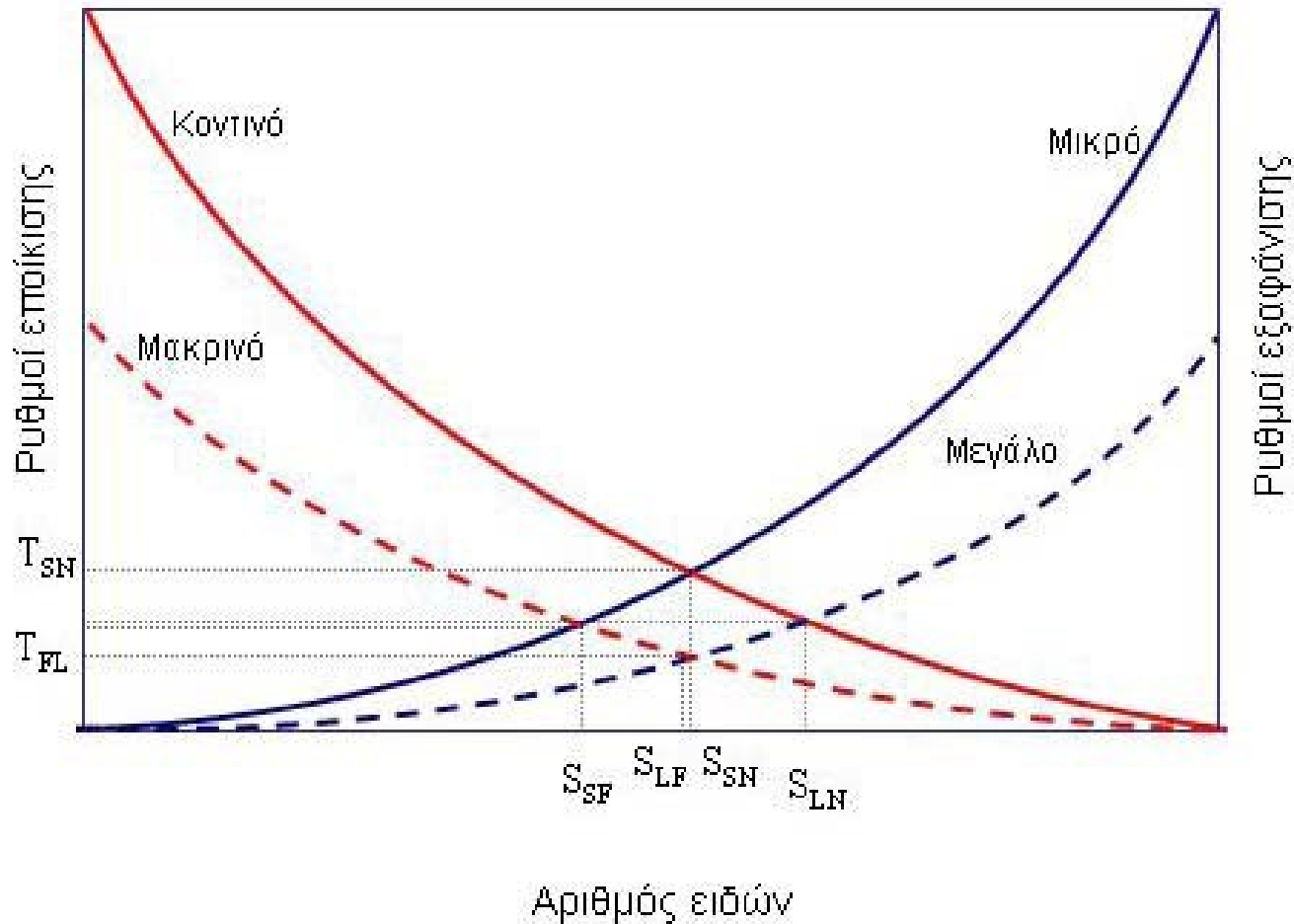
Biogeography

Small/large island

Near/far island

What to expect regarding:

- the number of species at the equilibrium point
- the replacement rates at the equilibrium point



MacArthur and Wilson's island equilibrium model shows the effect of island size (different extinction rate curves) and its degree of isolation (different colonization rate curves) on the number of species (S^{\wedge}) and turnover rates (T^{\wedge}) at equilibrium. The intercepts of the curves for islands of different combinations of extent and isolation can be used to predict the relative numbers of species and turnover rates at equilibrium.

Model checks

- Diamond counted, in 1969, the bird species on the islands off the coast of S. California, 50 years after the corresponding record by Howell (1917). The recording showed that the composition of species on these islands changed, but their species richness did not
 - In other words, during the 50 years between the two records, new species colonized the islands, while others ceased to inhabit it.
 - It was estimated that 20-60% of the species on each island were replaced from 1917 to 1969

Model checks

- Another example is research into the types of islands that formed during the opening of the Panama Canal, when land areas were flooded and turned mountain tops into islands. The results showed that
 - disappearances and colonizations are constantly repeated and
 - exchanges are smaller on the larger and more isolated islands



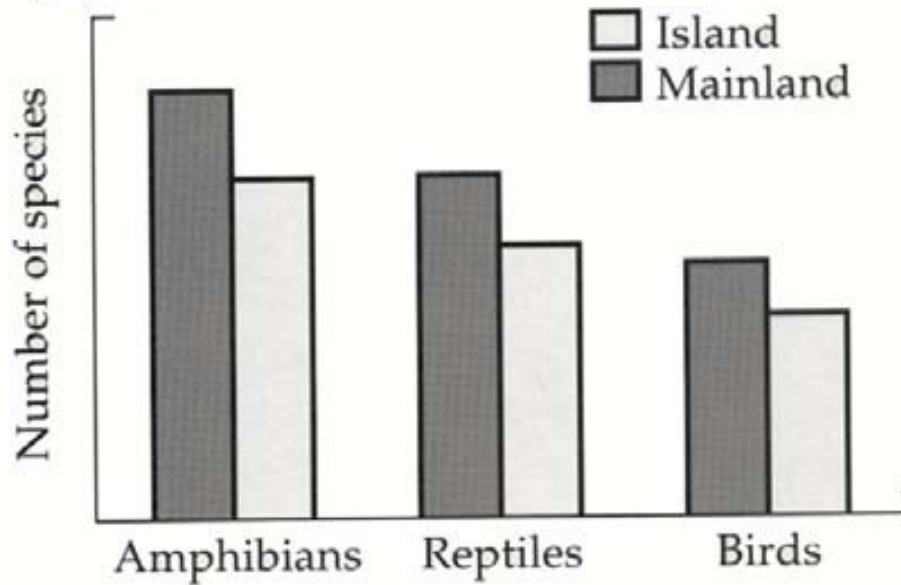
Model checks

- The most important test work of the theory was that of Wilson and Simberloff (1969, 1970) who carried out an experiment: without destroying the flora and using a special gas, they removed all arthropods (insects, spiders) from islands of mangrove vegetation in Florida. Their re - colonization was impressive.
 - Within a year, the arthropod communities were fully restored and even before equilibrium was reached, more species had colonized the islets.
 - The results were broadly consistent with the theory.

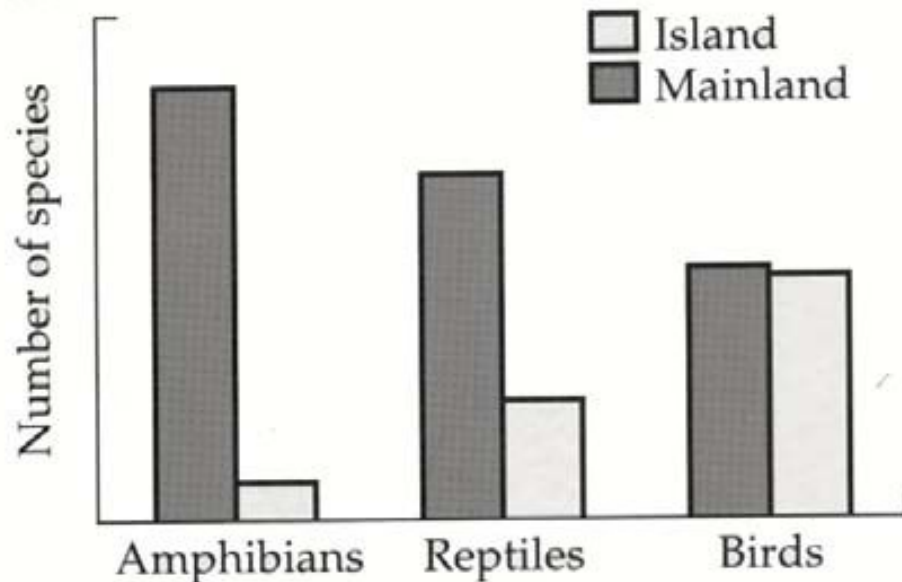
Structure standards

- Island **communities** tend to be **species poor** compared to mainland communities
- Usually **the composition of the communities on the islands is different** from that of their neighboring mainland areas that "feed" them.
 - That is, island communities are **disharmonic**
 - **Some** taxonomic, ecological or functional **groups are over-represented** , while some others, common to continental regions, are under-represented
 - The disharmony is most evident on the oceanic islands

(A) Harmonic biotas



(B) Disharmonic biotas



Two hypothetical examples of the pattern of species composition in harmonic and disharmonic island and mainland communities. In both categories, the island communities have fewer species of each group (amphibians, reptiles, birds). Disharmony, in disharmonic island communities, refers to the different composition of their communities (birds predominate and reptiles and amphibians fall short).

Biogeography

- This can be attributed to three factors:
 - to the selective nature of settlement
 - to the different ability to establish populations
 - and to the selective nature of extinction.

Selective nature of settlement

- Widely distributed species (birds, bats, insects) are better represented on islands than others with limited distribution (mammals, amphibians, reptiles)
- Also, plants or other organisms that disperse with birds are much more represented than other species, especially on oceanic islands
- The presence, on an island, of animals that cannot tolerate water salinity (freshwater fish and amphibians) is unlikely to be due to dispersal and is therefore an indication that the island was once part of a mainland

Biogeography

Different ability to establish populations

- Often, but not always, an increased ability to disperse is accompanied by a corresponding ability to settle or a more general ability to deal with a variety of environments
- Species with such traits are those that follow the **r strategy**
- These species are **adapted to the exploitation of disturbed** and newly formed **environments** and are characterized by a great dispersal capacity and resistance to a wide range of conditions

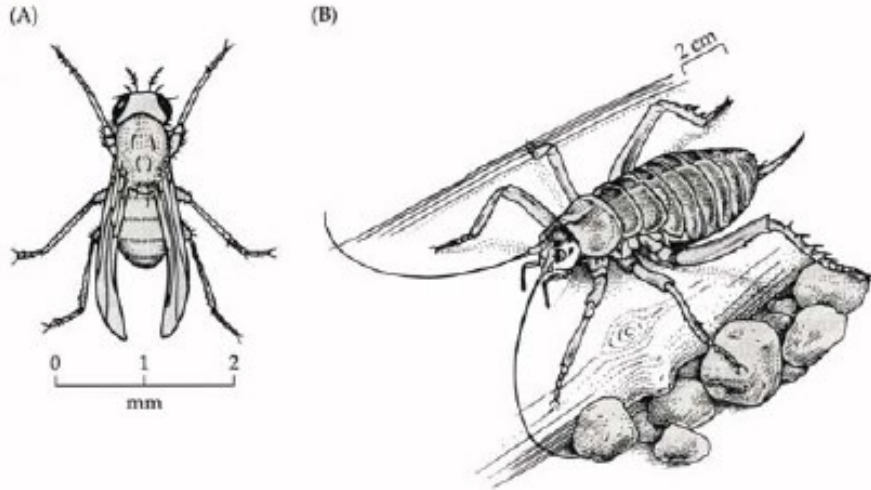
Selective nature of extinction

- A common feature for all islands is the **reduced provision of resources**, which is more pronounced the smaller the island.
- **those species that have low** resource requirements to maintain their populations are favored on the islands
 - Large carnivorous mammals, for example, are usually not present on small islands

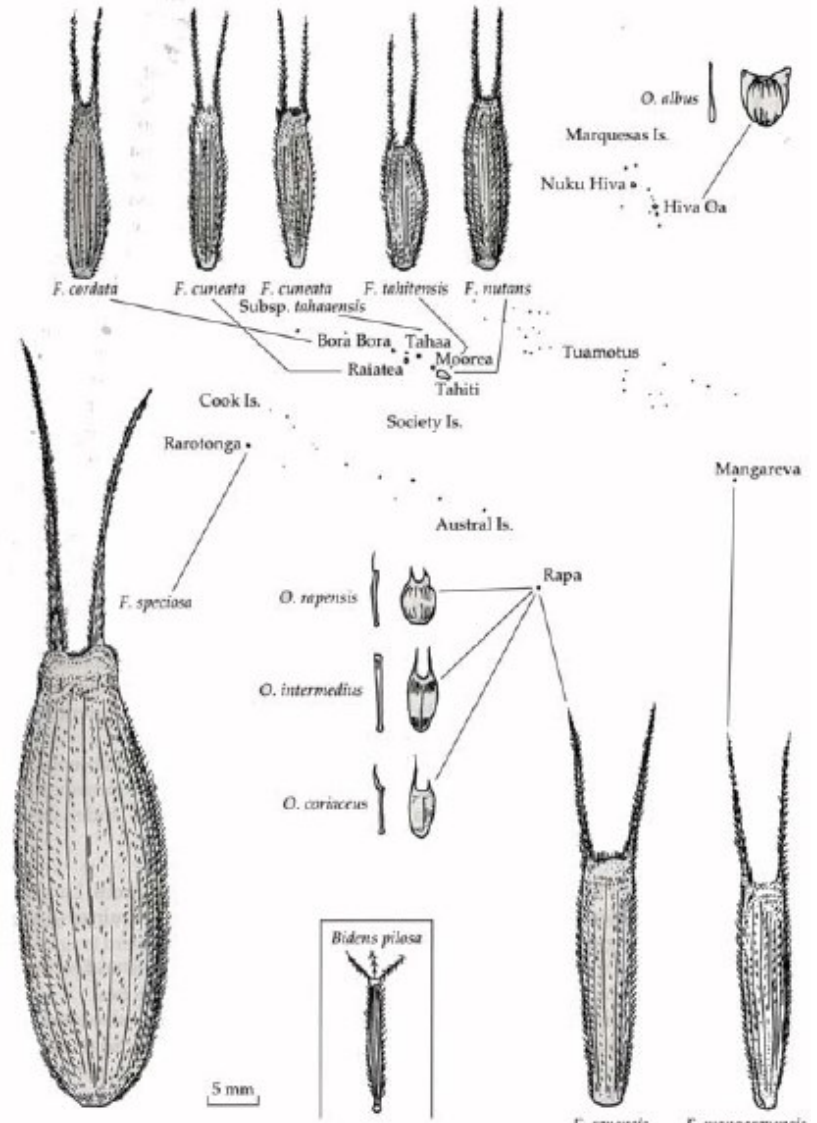
Evolutionary trends in the islands

Loss or reduction of dispersal ability

- Many oceanic islands are home to flightless bird and insect species
- These organisms are descendants of others who were able to fly to colonize these islands
 - evolutionarily they lost this ability, which was now useless
 - 25-35% of the land and water birds of S. Zealand
- A reduction in dispersal ability is also a common phenomenon in many plant island species



Examples of two species of insects that live on islands and have lost the ability to fly. (A): *Scaptomyza frustulifera*, a species of fly, a relative of *Drosophila* and (B): *Deinacrida rugosa*, orthopteran, ecologically equivalent to rodents. The latter was displaced from New Zealand and other coastal islands after the introduction of rats, mice and other terrestrial mammals.



On islands, the seeds and fruits of many plants bear traits that indicate little ability to spread (e.g., they become heavier, cannot float, are less resistant to seawater, bear fewer thorns or wings, and generally do not bear structures that facilitate attachment to animals). The image shows the relatively large sizes and shapes of the fruits of species of the genera *Fitchia* and *Oparanthus*. In the inset, for comparison, the small fruit size of *Bidens pilosa* which shows a more continental morphology.

Evolutionary trends in the islands

Changes in body size

- Quite often island organisms are much larger or much smaller than their mainland relatives -
> gigantism and dwarfism
- Body size on the islands, but also in general, offsets some benefits and some costs
 - Larger individuals can exploit a greater variety of resources (eg consume both large and small food sizes)
 - The small size gives other advantages: e.g. smaller animals have fewer resource demands

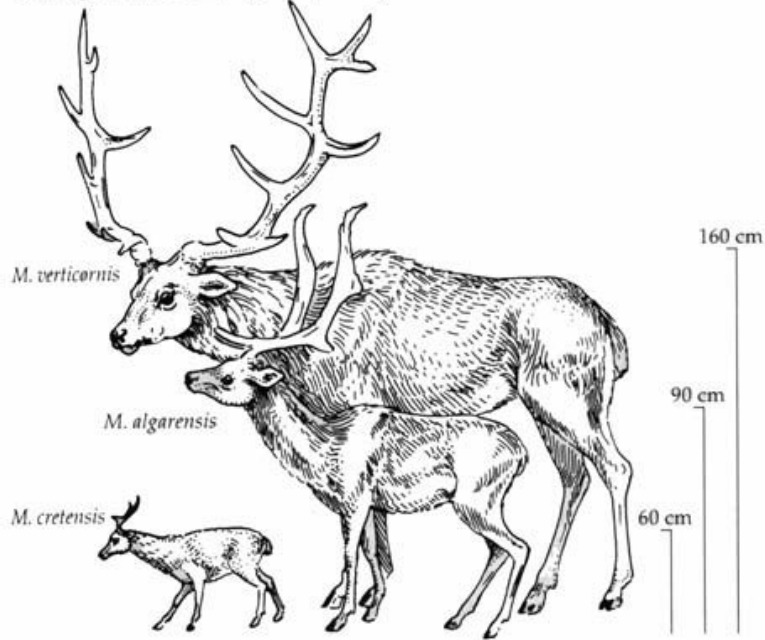
Evolutionary trends in the islands

Mamals

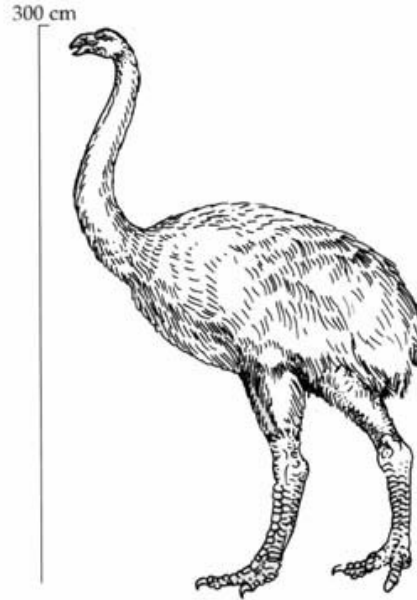
- For island mammals, the following island rule seems to apply, in general:
 - large mammals (large carnivores and herbivores, such as the pygmy mammoth also found on Mediterranean islands) tend to decrease in size, while small mammals (e.g. rodents) tend to increase in size



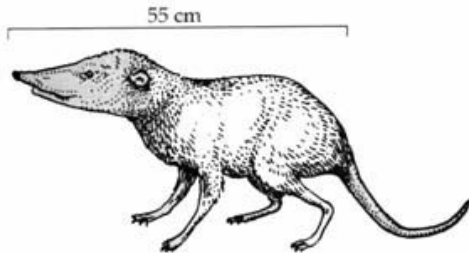
Dwarfing in Giant Deer (*Megaceros*) during the Pleistocene



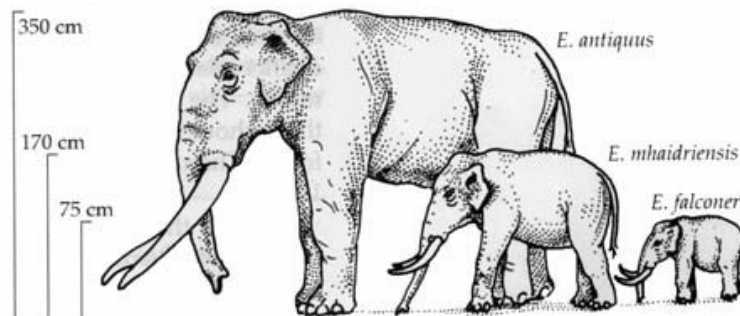
One of the now extinct Moas (*Diornis giganteus*) of New Zealand (1,500 years B.P.)



Giant Shrew (*Deinogalerix koenigswaldi*) of Southern Italy (15–20 million years B.P.)



Dwarfing in Elephants (*Elaphus*) during the Pleistocene



Insular forms of mammals often exhibit trends of morphological divergence, fluctuating from dwarfism in large mammals such as elephants and deer to gigantism in small rodents and birds.

Biogeography & Ecology Laboratory
Department of Geography
University of the Aegean



POL-AEGIS

The pollinators of the Aegean: diversity & threats



αἰγίς, ἴβω, ἴ:
goddess, wears as a dress; esp. the skin shield of Zeus, lent by him to Athena; later, with fringe of
snakes and Gorgon's head, the aegis of Athena

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Dwarfism in the bees of the Aegean Archipelago

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European Union
European Social Fund



MINISTRY OF EDUCATION & RELIGIOUS AFFAIRS
MANAGING AUTHORITY

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Island Rule

- **Geographic isolation on islands leads to genetic isolation**
- **Evolutionary differentiation of body size (gigantism / dwarfism)**
- **Possible explanation**
 - **for gigantism: absence of predators or competitors in island communities**
 - **for dwarfism: resource limitation**

Island Rule

- **It was mainly studied by comparing island species with their closest relatives on the mainland**
- **It has rarely been studied on the basis of comparison of populations of the same species and never at the community level**

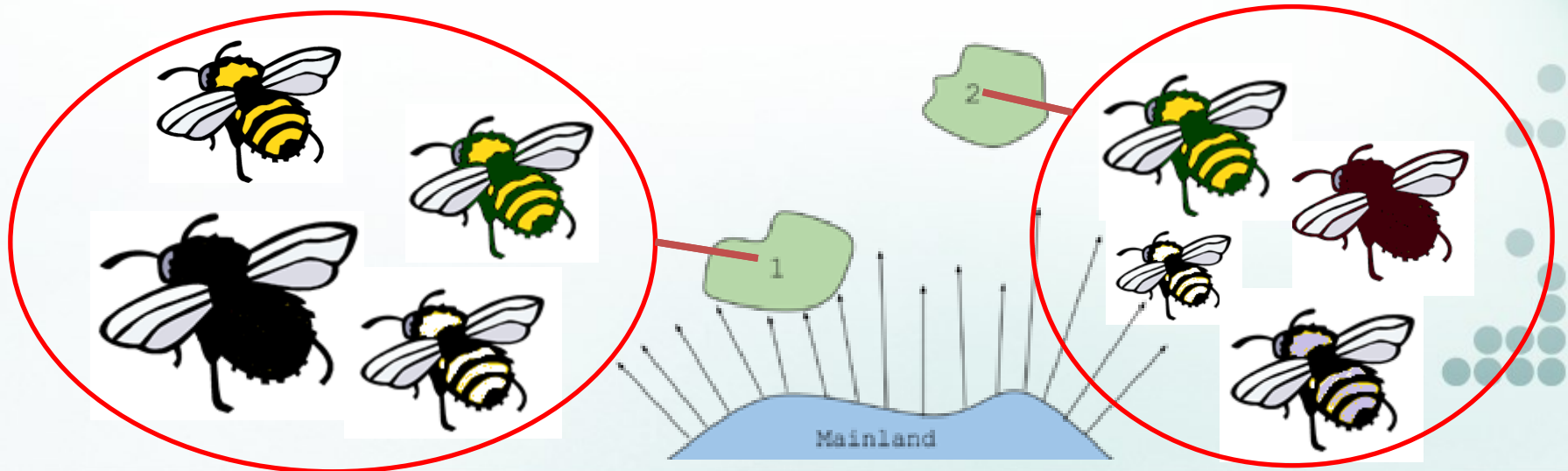
Research questions

1) Does the average size of bee species per island depend on the size of the island?



Research questions

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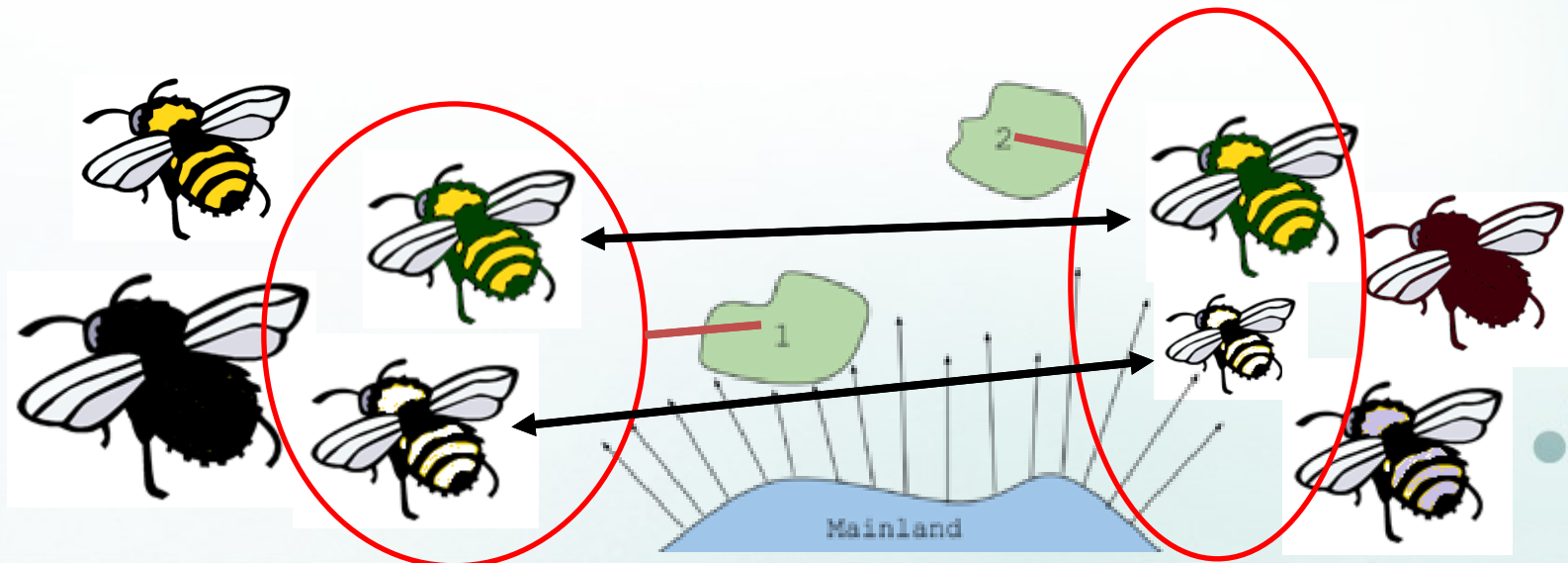


Research questions

- 1) Does the average size of bee species per island depend on the size of the island?
- 2) Do the sizes of common species depend on the size of the island?**

Research questions

- 1) Does the average size of bee species per island depend on the size of the island?
- 2) Do the sizes of common species depend on the size of the island?



Methodology

1) Sampling with pantraps at 217 points, on 24 islands of the Aegean Archipelago

Aegina, Anafi, Heraklion, Thassos, Ikaria, Ios , Karpathos, Kea, Kos, Lesvos, Limnos, Milos, Mykonos, Naxos, Paros, Rhodes, Samothrace, Santorini, Serifos, Sifnos, Syros, Tinos, Chios, Folegandros



Methodology

1) Sampling with trapdoors and traps

2) Measuring the size of bees

- 5 females per species and island
- Intertegular Distance (ITD)



Methodology

1) Sampling with trapdoors and traps

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- 5 females per species and island
- Intertegular Distance (ITD)



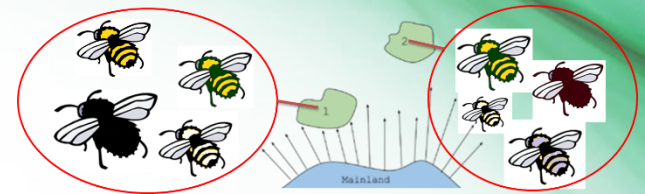
Methodology

1) Sampling with trapdoors and traps

2) Measuring the size of bees

3) Calculation of variables

- Average size of species per island



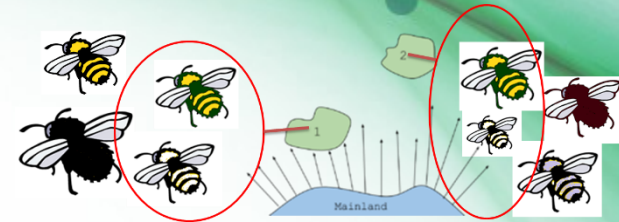
Methodology

1) Sampling with trapdoors and traps

2) Measuring the size of bees

3) Calculation of variables

- Average size of species per island
- Average relative size difference per island



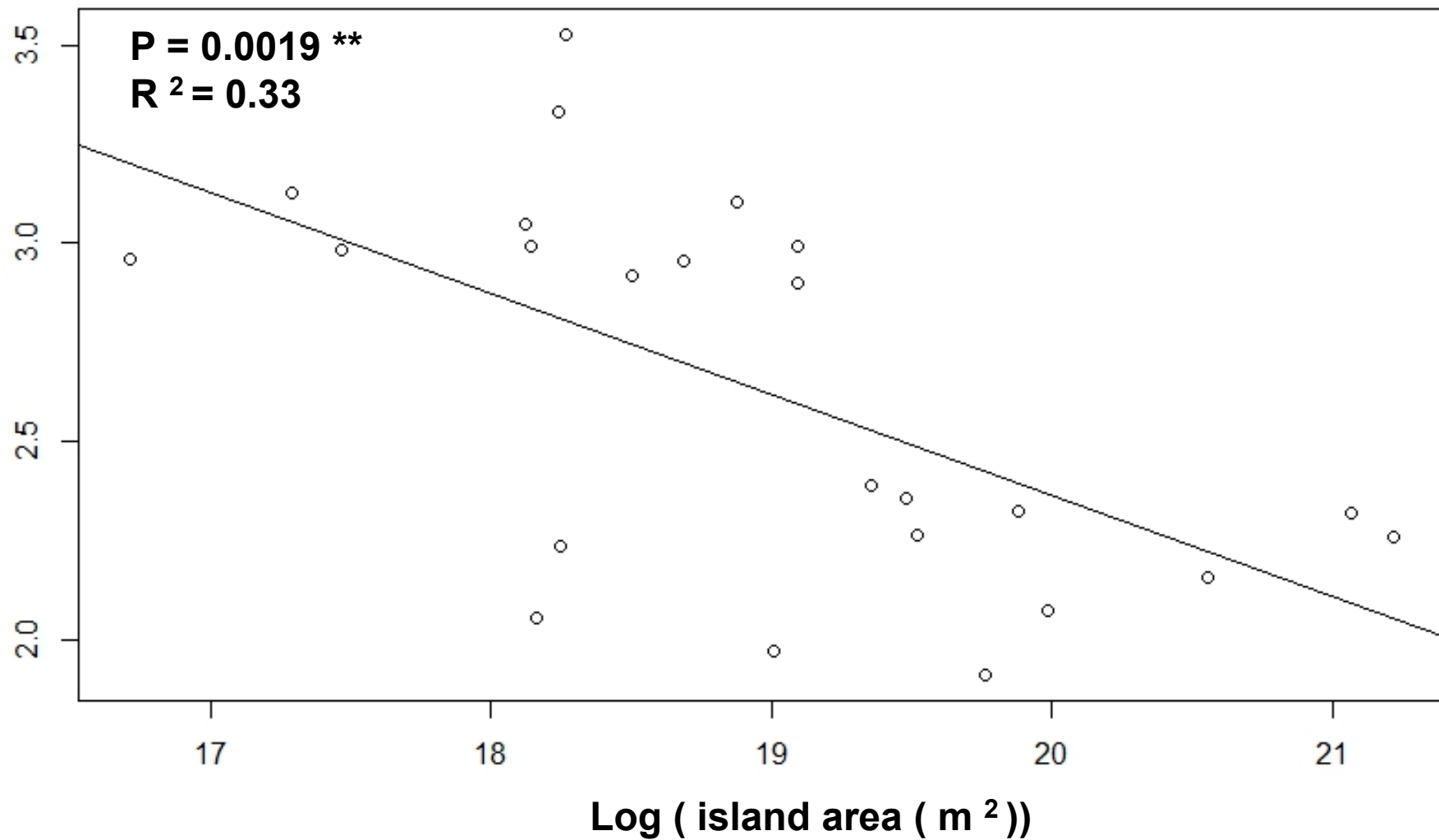
Results

1) 450 species of bees were collected

2) Small islands host fewer, but overall larger bee species



Mean size (ITD) of species per island in mm



Results

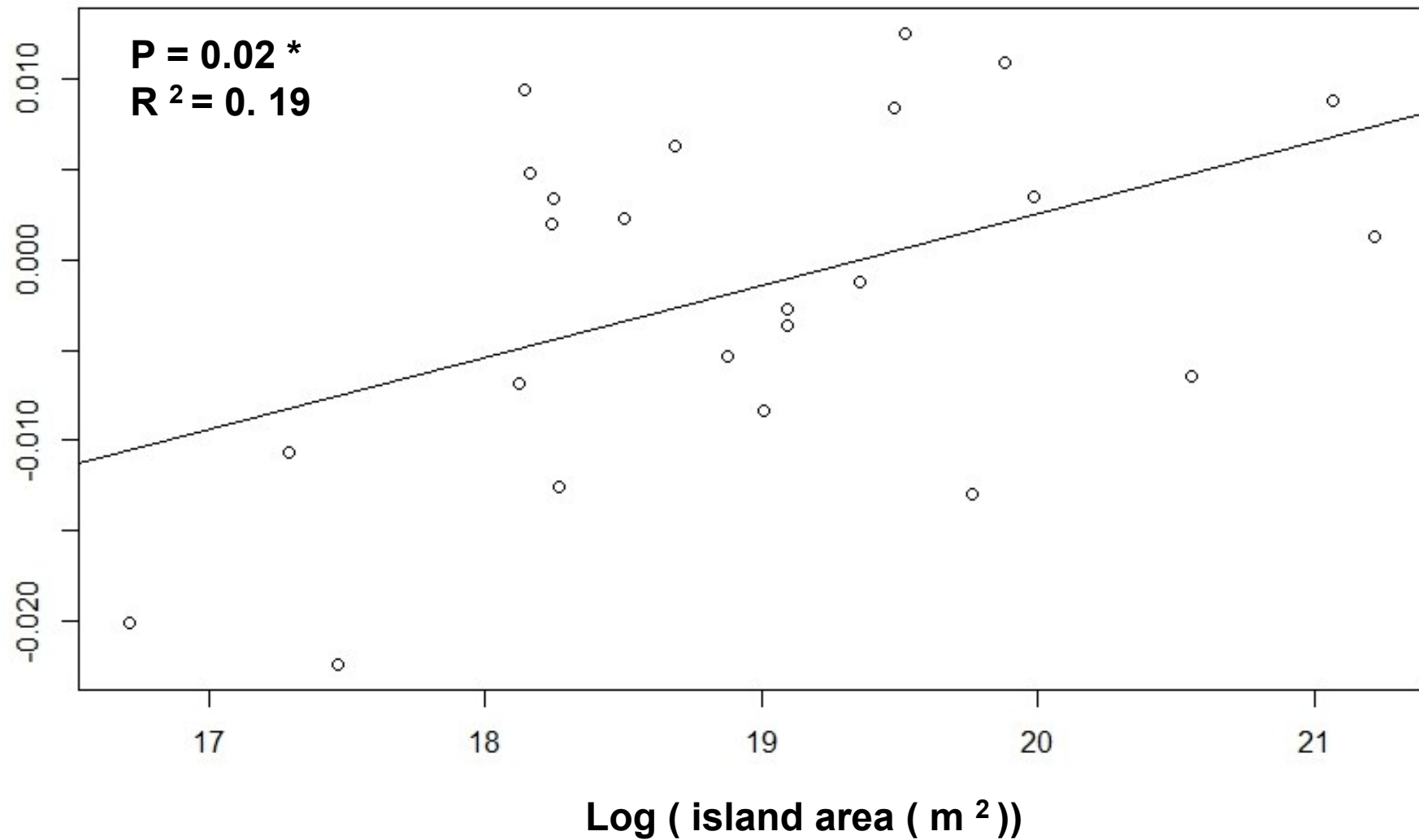
1) 450 species of bees were collected

2) Small islands host fewer but overall larger bee species

3) Individuals of the same species are relatively smaller on small islands



Relative size difference (ITD) per island



Conclusions & Discussion

- **The average size of bee species per island depends on the size of the island**
 - **Small islands -> large species**
 - **Possible explanation: large species have greater dispersal capacity**

Conclusions & Discussion

- The average size of bee species per island depends on the size of the island
- **The sizes of common species depend on the size of the island**
 - **Small islands -> small individuals per species**
 - **Possible explanation: limited resources**

Conclusions & Discussion

- The average size of bee species per island depends on the size of the island
- The sizes of common species depend on the size of the island
- **Evolutionarily the process of dwarfism can happen relatively quickly**
 - **It agrees with the relatively short period of time that most of the Aegean islands are isolated**

Future Research

- 1) Do bee taxa respond differently?**
- 2) Do functional groups respond differently?**
- 3) Are differences in size genetic or environmental?**
- 4) Is it related to the size of the flowers on the islands?**
- 5) What is the role of distance (from neighboring areas)?**
- 6) Switching islands (stepping stones)?**

Thank you for your interest

