Lecture 10

Dynamics of Biodiversity and Theory of Island Biogeography

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Outline

1. Species succession on Karakatau

2. Biogeographic definition of oceanic vs. continental islands

3. Theory of island biogeography

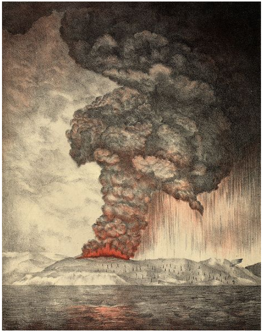
The Karakatau eruption of 1883 and its aftermath

Before 1883, Karakatau was a volcanic island in the Sunda strait between Sumatra and Java, in nowadays Indonesia.

Krakatau as it appeared 15 days before the paroxysmal eruption; width of Rakata Island is about 5 km. Map by H. J. G. Ferzenaar.

The Karakatau eruption of 1883 and its aftermath

In May 1883, Karakatau started a sequence of eruptions, culminating on 27 August with an exceptionally strong eruption that destroyed most of the island – causing tsunamis that resulted in 36000 casualties, and affecting global climate because of the huge amount of volcanic ash thrown into the atmosphere.

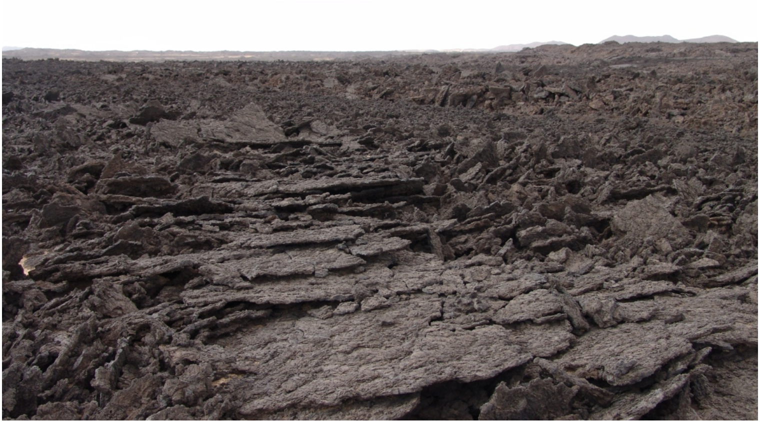


The Karakatau eruption of 1883 and its aftermath

What was left of Karkatau island is now called Rakata island. It is part of the Karakatau group, including Rakata, Panjang and Sertung. In 1927, a new volcanic island, Anak Karakatau, has started to form in the middle of the island group. By 1990s Anak Karakatau has grown to be 300m high and 2km wide.

The Karakatau eruption of 1883 and its aftermath

All plant and animal life has been completely exterminated during the 1883 eruption. The islands were buried in volcanic ash, several meters deep. This set the stage for colonization of the sterilized islands by a fresh new biota.



Species succession on Rakata island

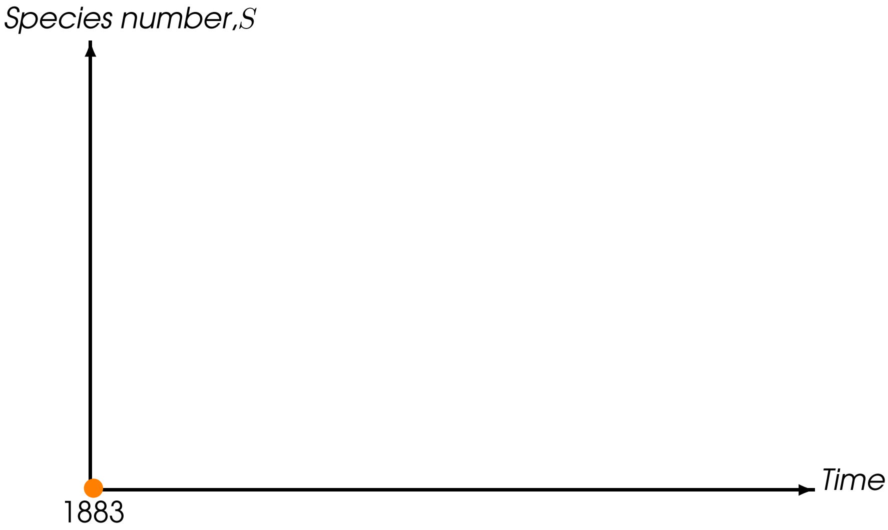
As different groups of plants and animals colonize the islands, a clear order of arrival and establishment can be observed – a process called **succession**.

We will concentrate on succession of plant species, but similar patterns are observed in birds and butterflies.

As clearly seen in the photo, Rakata island nowadays – 130 years after it became a sterile volcanic wasteland – is covered in thick forest. How did it come about?

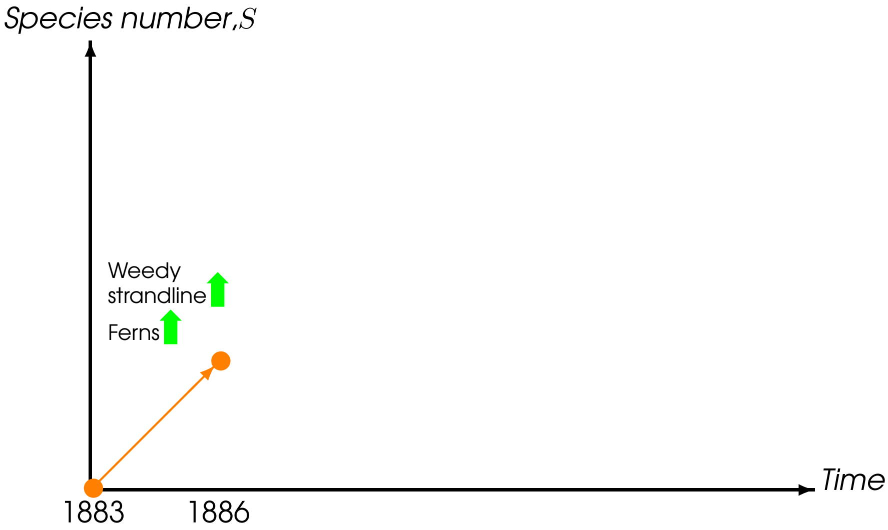
Species succession on Rakata island

1883: Island is sterilized, $S = 0$. In following years, several expeditions surveyed the recovery of plant and animal life.



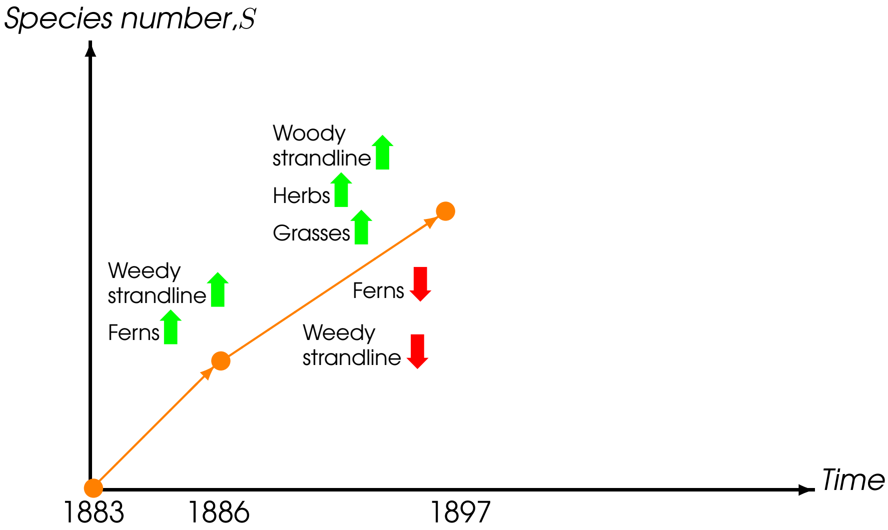
Species succession on Rakata island

1886: Wind-dispersed ferns (microscopic spores) and strand-line (sea-dispersed) herbaceous plants on coasts.



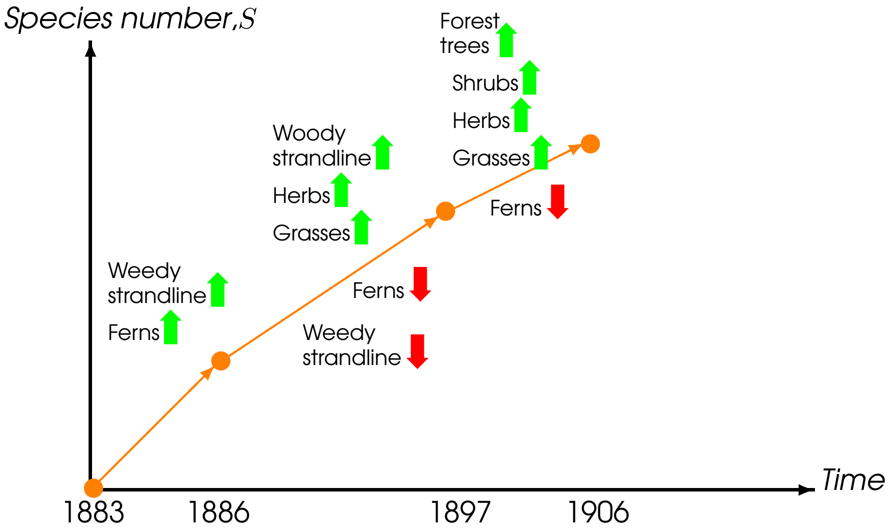
Species succession on Rakata island

1897: Grasses and herbs (e.g., Asteraceae) start to take over the interior and replace the fern cover. Woody strandline plants establish.



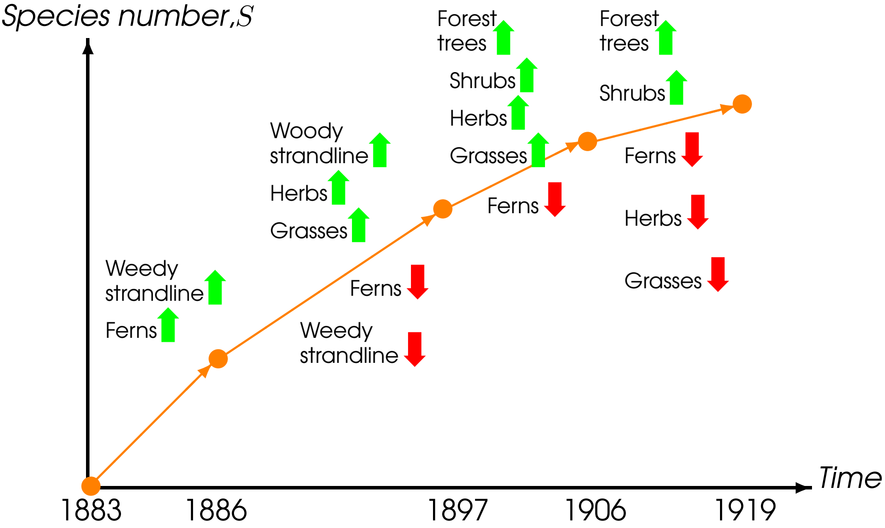
Species succession on Rakata island

1906: Grasslands in the interior replace the ferns. Isolated shrubs and trees start to appear – seeds brought by birds.



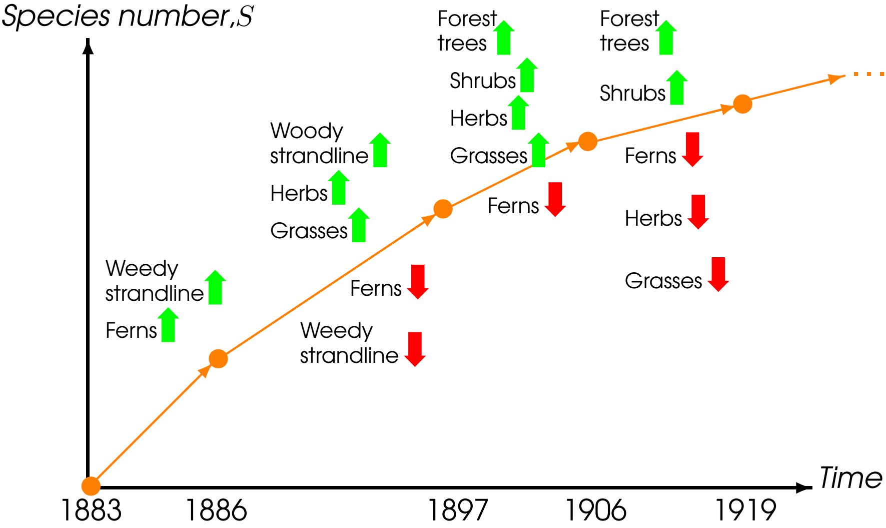
Species succession on Rakata island

1919: Grasslands start to recede in favor of increasing areas of forest.



Species succession on Rakata island

1920s-30s: Forest closure. Most of the island covered in forest. Very little open habitat (grasslands) remains.



Summary of succession on Rakata island

- Rakata is a **continental** island, close to two much larger mainlands – Java and Sumatra.
- Note that, similar to evolution of plant species on oceanic islands, in the succession process there is also a transition over time from more weedy/herbaceous species to more woody species.
- However:
  1. The transition through succession occurs much faster – decades rather than tens of thousands of years.
  2. The transition occurs not by a weedy ancestor evolving and speciating into more woody species – But by woody species immigrating from the mainland and replacing more herbaceous species.
- Trees are less dispersive, so they arrive later – but they do arrive eventually. Unlike the case on oceanic islands.

Summary of succession on Rakata island

- Following the devastation of the 1883 eruption, the number of plant species started to increase over time.
- At first, at a fast pace, as wind- and sea-dispersed species arrived and colonized quickly (ferns and coastal species).
- Later, the rate of increase in species number became slower and slower.
- There are two types of reasons for that:
  1. **Statistical** – the more species there are already on the island, the less likely that an incoming immigrant would be of a new species.

Summary of succession on Rakata island

- There are two types of reasons for that:
  1. **Statistical** – the more species there are already on the island, the less likely that an incoming immigrant would be of a new species.
  2. **Biological** –

     (i) **Immigration rate –** With more species already occupying the island, there are **less empty niches and habitats** available for new colonizers. Establishment of new immigrants on the island requires successful competition with an increasing number of resident species.

     (ii) **Extinction rate –** Competition and change in the environment (e.g., barren land → grassland → closed forest) cause some species to decline and go extinct
     $\Rightarrow$ There is not only **gain** of species through immigration, but also **loss**, because some go extinct.
     $\Rightarrow$ Extinction decreases **net** gain in species.

Summary of succession on Rakata island

- *Conclusion 1*: Change in species number over time is determined by processes that increase species number – **immigration** (הגירה) and **evolution** – and processes that decrease it – causing (local) **extinction** (הכחדה) of species.
- *Conclusion 2*: In theory, at some point a balance or **equilibrium** (שיווי משקל) may be reached – resulting in zero **net** change in species number, although the identity of the species may still change, because arrival of new species and extinction of resident species continue to occur.
- This kind of equilibrium is called **dynamic equilibrium** (שיווי משקל דינמי).
  (Like when the amount of money in your bank account does not change if your income exactly balances your expenses.)

Outline

1. Species succession on Karakatau
2. Biogeographic definition of oceanic vs. continental islands
3. Theory of island biogeography

The biogeographic classification of islands

- We are already familiar with the geological definitions of oceanic and continental islands.

Oceanic vs. Continental (shelf) Islands

Continental (shelf) islands

- Rise from continental crust (continental shelf)
- Mixed origin and rock types.
- May have been connected to mainland.
- Britain, Ireland, Indonesian islands of the Sunda shelf, Sri Lanka, Malta.

Oceanic islands

- Rise from oceanic crust.
- Invariably volcanic in origin (basaltic).
- Have never been connected to mainland.
- Hawaii, Galapagos, Canary islands, Azores, Mauritius, Easter island.

The biogeographic classification of islands

- We are already familiar with the geological definitions of oceanic and continental islands.
- A biogeographic classification of islands is based on the different processes that determine biodiversity on islands – specifically, species number, ***S***.

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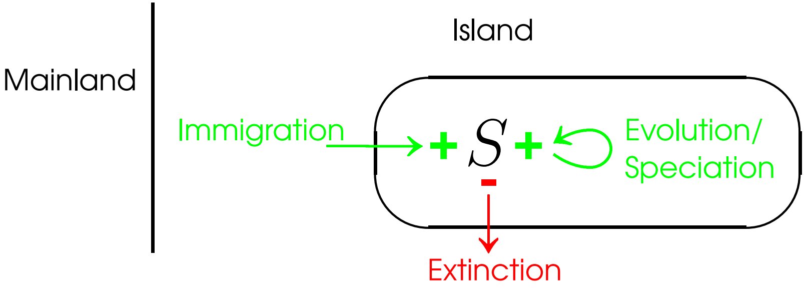

The biogeographic classification of islands

Far from mainland – oceanic island:

Close to mainland – continental island:

The biogeographic classification of islands

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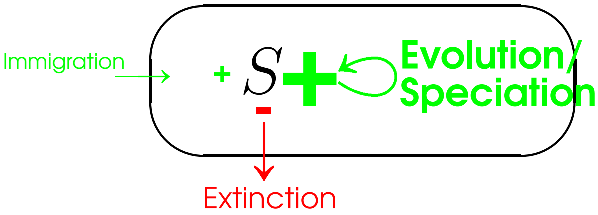
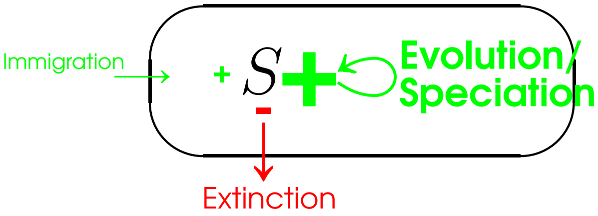


Close to mainland – continental island:

The biogeographic classification of islands

Far from mainland – oceanic island:



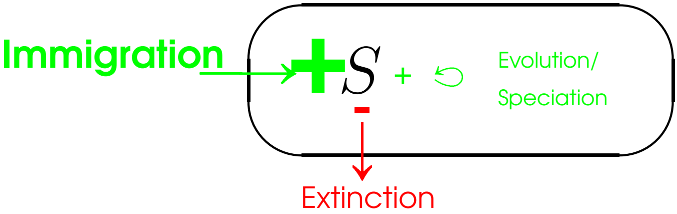
Immigration

+ S **+** **Evolution/ Speciation**

−

Extinction

Close to mainland – continental island:



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Extinction

The biogeographic classification of islands

- The biogeographic classification of islands is based on the relative importance of evolution vs. immigration.

- On an oceanic island, rate of evolution/speciation is faster than rate of immigration.
- ⇒ Island biota changes through evolution of new species that may replace old species – i.e., through speciation.

- On a continental island, rate of immigration is faster than rate of evolution/speciation.
- ⇒ Island biota changes through new species immigrating to the island and potentially replacing resident species – i.e., through species turnover and succession.

- Overall, the rate of change in biotas would be much faster on continental islands (decades vs. thousands of years on oceanic islands).

What about extinction rates?

- In general, the more individuals we have of a species, the less likely it is that the species would go extinct.
- ⇒ Larger islands can support larger populations, and therefore, **extinction rate should decrease as island area increases.**

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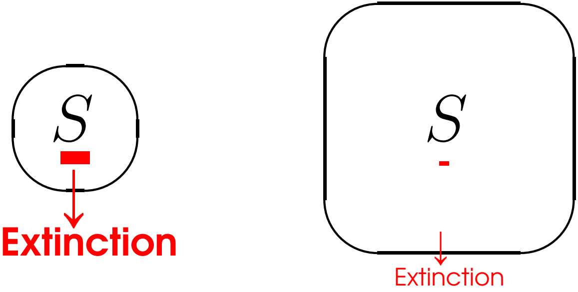

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Theory of island biogeography (TIB)

- The focus is now continental islands.
- Immigration is more important than evolution in increasing species number on islands.
- We ignore evolution (the time scale of island colonization is years to decades).
- Changes in species number is determined by immigration from mainland and by (local) extinction on island.
- We have already seen that rate of change in species number is not constant, but itself varies over time.
- In 1967, Robert McArthur and Edward Wilson published the “Theory of island biogeography”, in which they presented a graphical/mathematical model for the dynamics of species numbers on islands. – It became one of the most influential theories in Ecology.

Species succession on Rakata island

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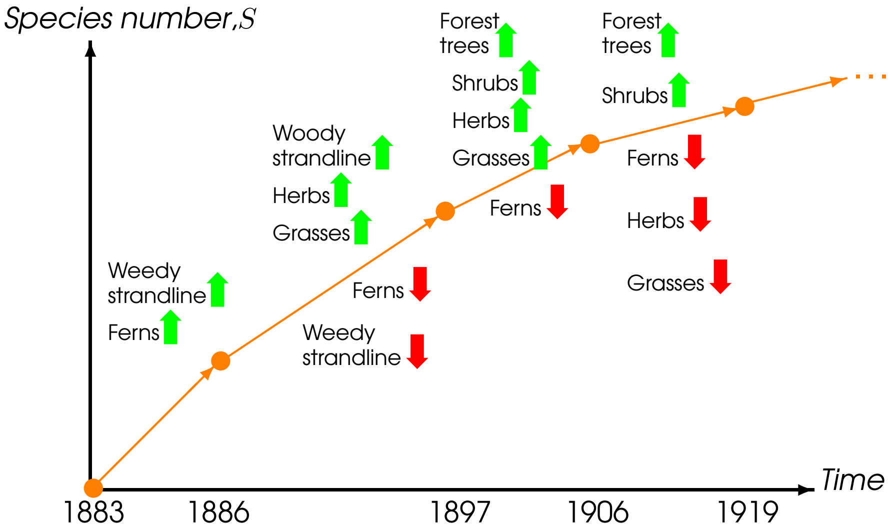

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          ⇒ There is not only **gain** of species through immigration, but also **loss**, because some go extinct.
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Theory of island biogeography (TIB)

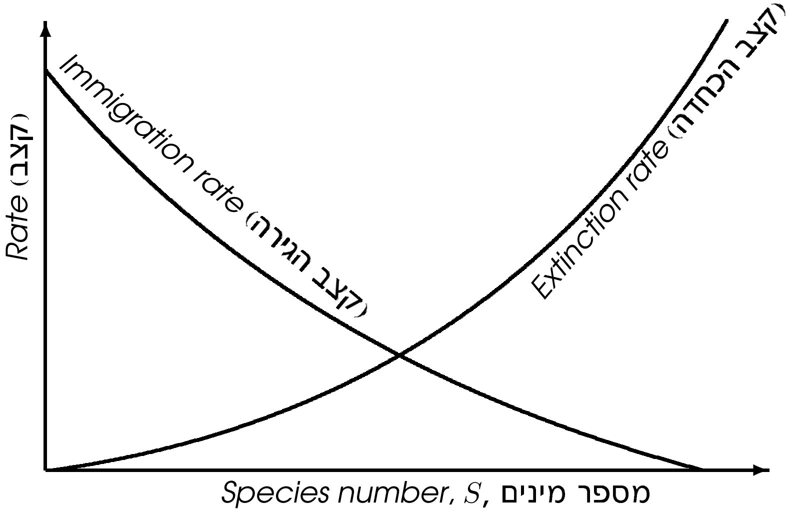
We can describe the relation of immigration rate or extinction rate to species number in a graphical way.

Theory of island biogeography (TIB)

Immigration rate should decrease as species number, S, increases.

Theory of island biogeography (TIB)

While extinction risk should rise as S increases.



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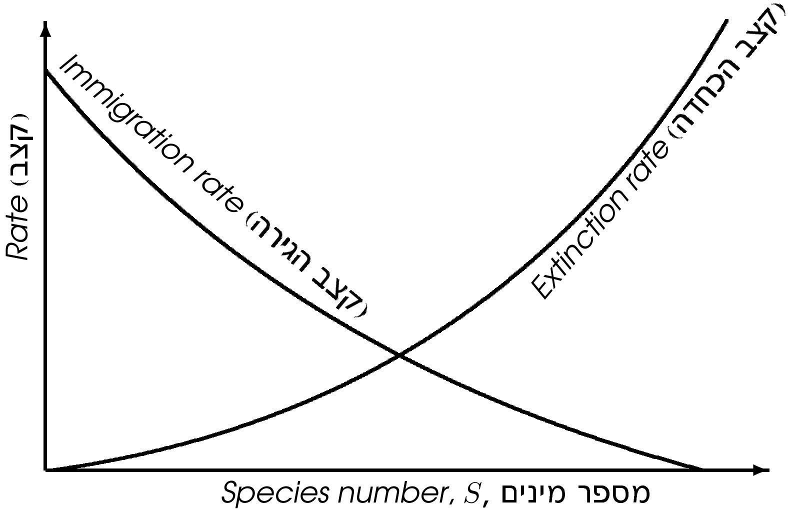
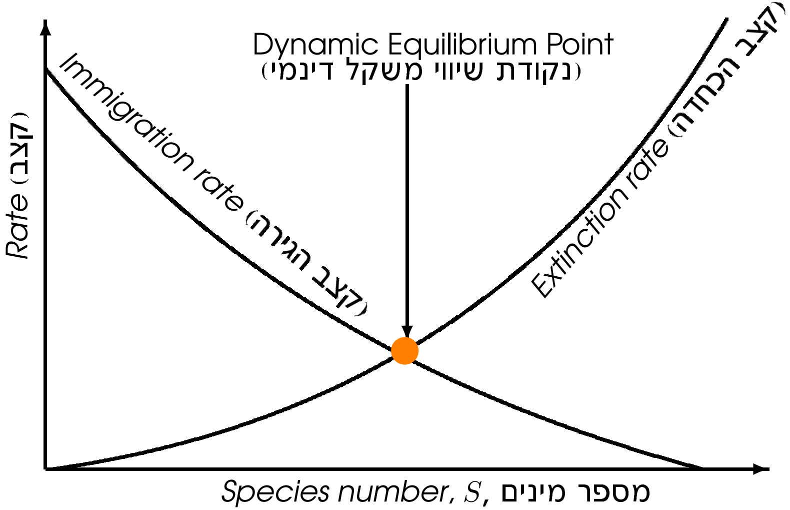


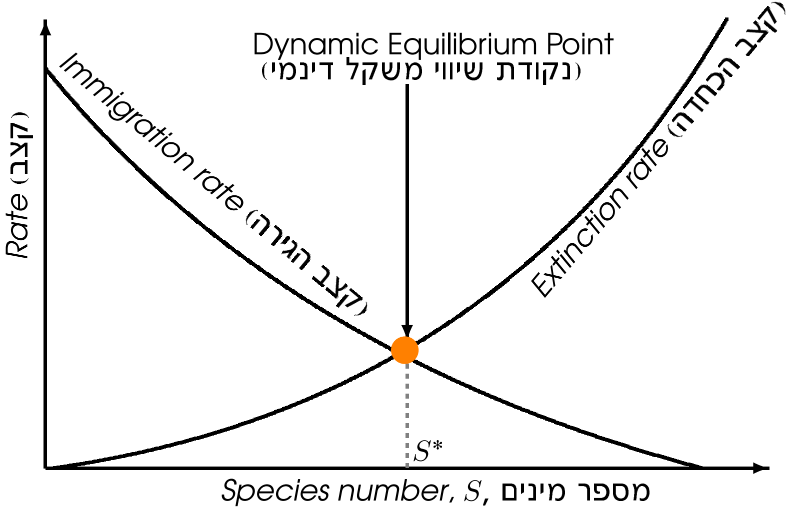
Theory of island biogeography (TIB)

Where extinction balances immigration, we get the point of dynamic equilibrium.



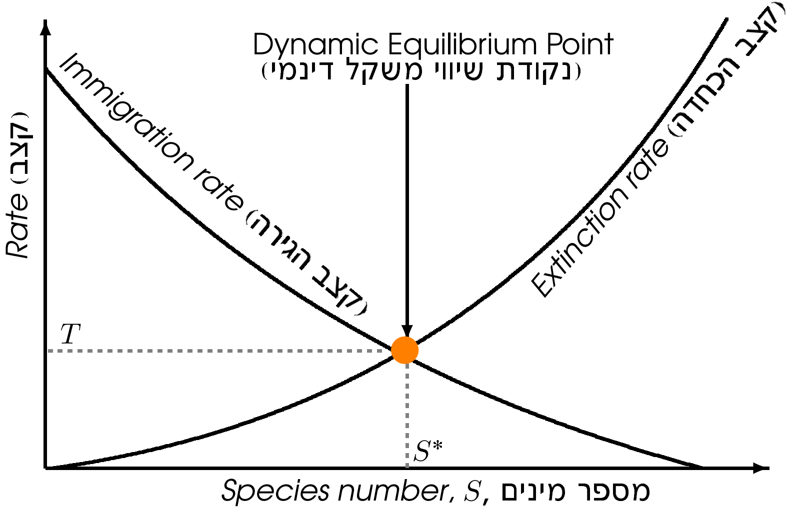
Theory of island biogeography (TIB)

Equilibrium point defines S^*, the species number at equilibrium . . .



Theory of island biogeography (TIB)

and defines T, the **turnover rate** of species at equilibrium.

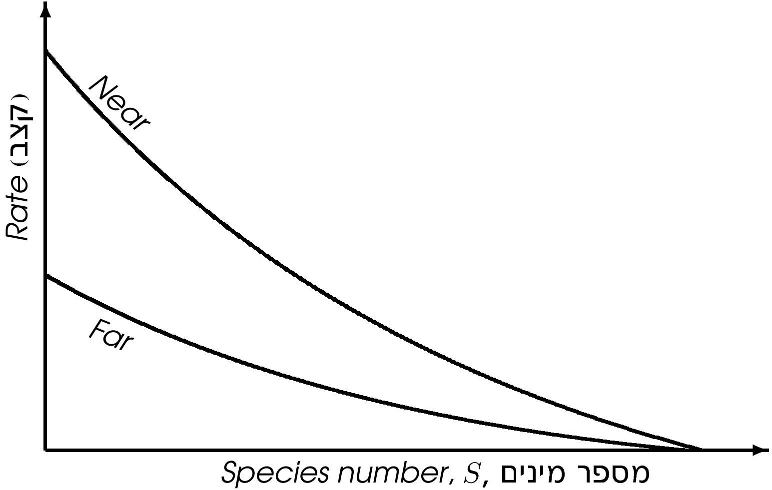


Theory of island biogeography (TIB)

- Species turnover rate (קצב תחלופת מינים), T, is the rate at which the composition of species changes over time.
- At equilibrium, the total number of species, $S*$, remains constant. But the species composition, or the identity of component species, change over time, at a rate T.
- We can explore how $S*$ and T change in different situations.

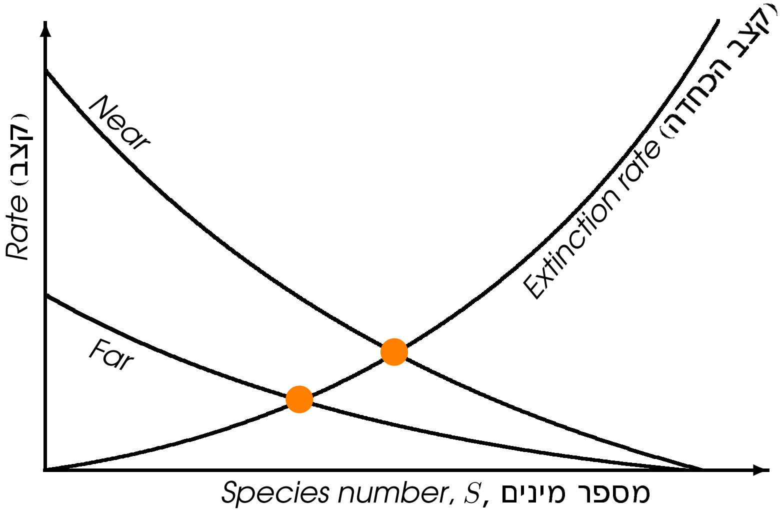
Theory of island biogeography (TIB)

In TIB, immigration rate is affected by distance – decreases with distance from mainland.



Theory of island biogeography (TIB)

$\Rightarrow S^*(Near) > S^*(Far)$ and $T(Near) > T(Far)$.



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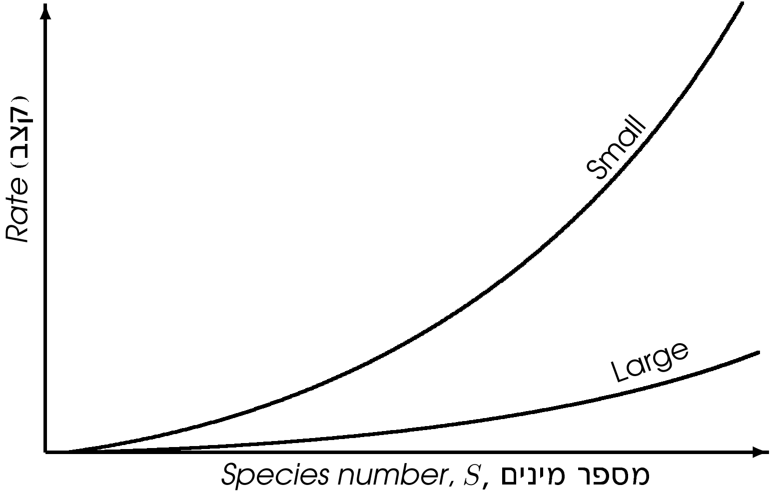
- We can explore how $S*$ and T change in different situations.
- Immigration decreases with distance $\Rightarrow$ the farther the island, the lower is equilibrium species number and the slower is species turnover.

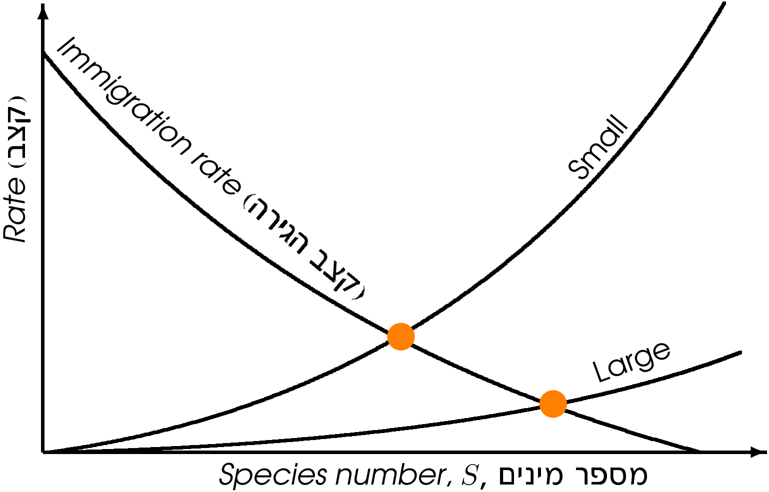
Theory of island biogeography (TIB)

In TIB, extinction rate is affected by island size – decreases with the size of the island.



Theory of island biogeography (TIB)

$\Rightarrow S^*(Large) > S^*(Small)$ and $T(Large) < T(Small)$.

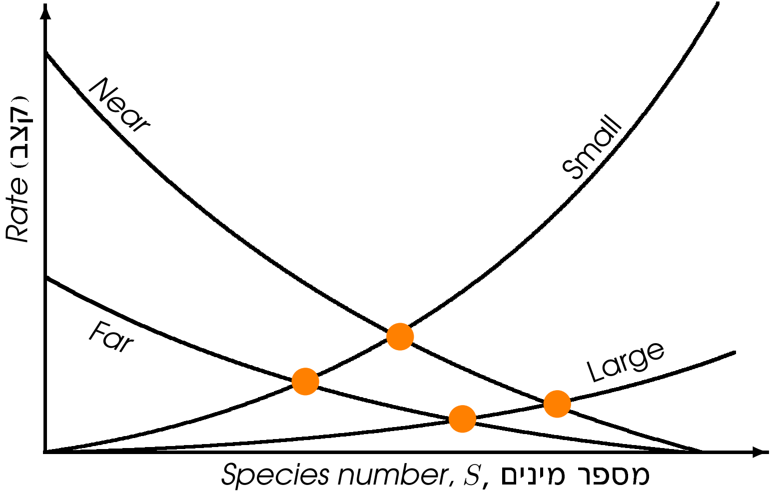


Theory of island biogeography (TIB)

- Species turnover rate (קצב תחלופת מינים), T, is the rate at which the composition of species changes over time.
- At equilibrium, the total number of species, $S*$, remains constant. But the species composition, or the identity of component species, change over time, at a rate T.
- We can explore how $S*$ and T change in different situations.
- Immigration decreases with distance ⇒ the farther the island, the lower is equilibrium species number and the slower is species turnover.
- Extinction decreases with area ⇒ the larger the island, the higher is equilibrium species number and the slower is species turnover.

Theory of island biogeography (TIB)

$$S*(Near, Large) > S*(Near, Small), S*(Far, Large) > S*(Far, Small)$$
$$T(Near, Small) > T(Near, Large), T(Far, Small) > T(Far, Large).$$



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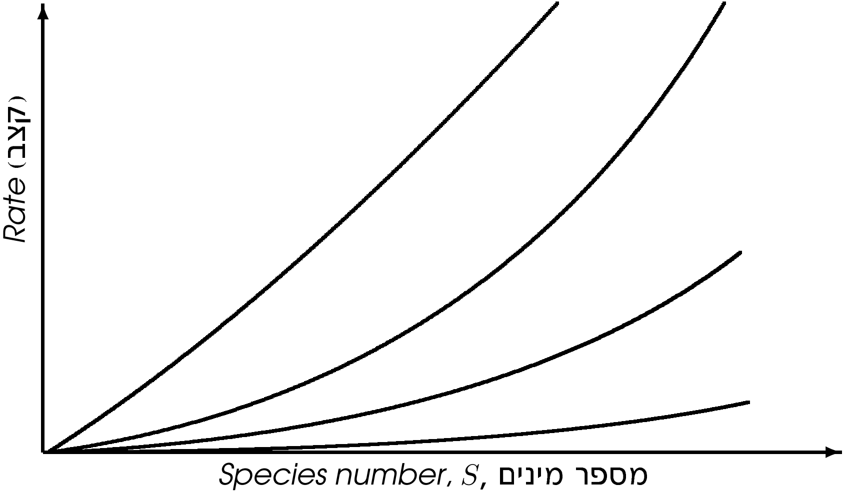
- We can explore how $S*$ and T change in different situations.
- Immigration decreases with distance ⇒ the farther the island, the lower is equilibrium species number and the slower is species turnover.
- Extinction decreases with area ⇒ the larger the island, the higher is equilibrium species number and the slower is species turnover.
- TIB provides general predictions on how species number and turnover rate should change with island characteristics (Near/Far, Large/Small).

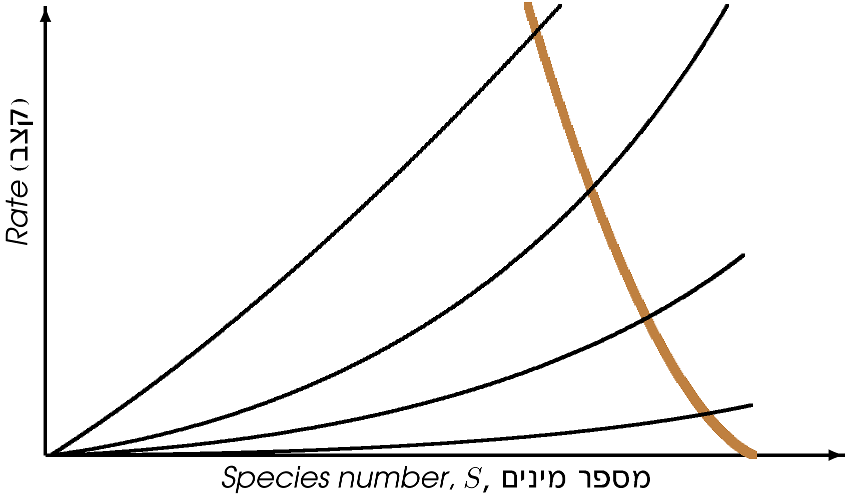
Application of TIB to species-area relations (SAR)

Several areas, each of a different size, and therefore, different extinction rate curve.



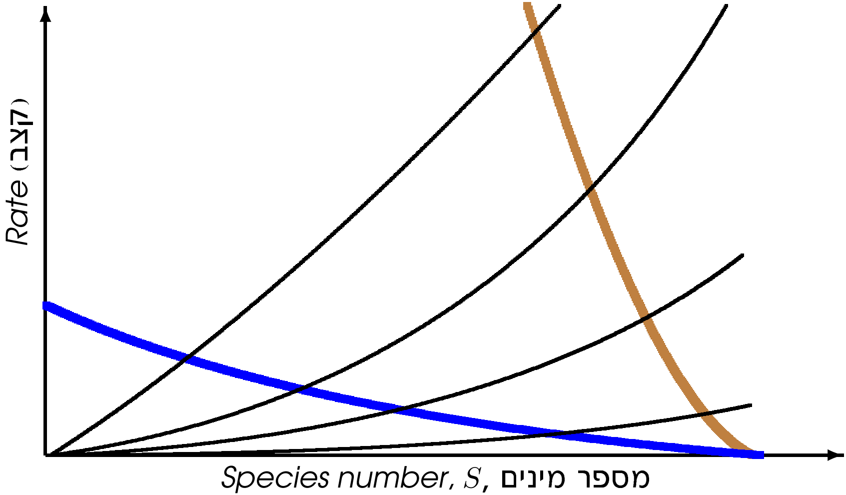
Application of TIB to species-area relations (SAR)

If the different areas are within a continent ⇒ high immigration rate, because isolation is very low.



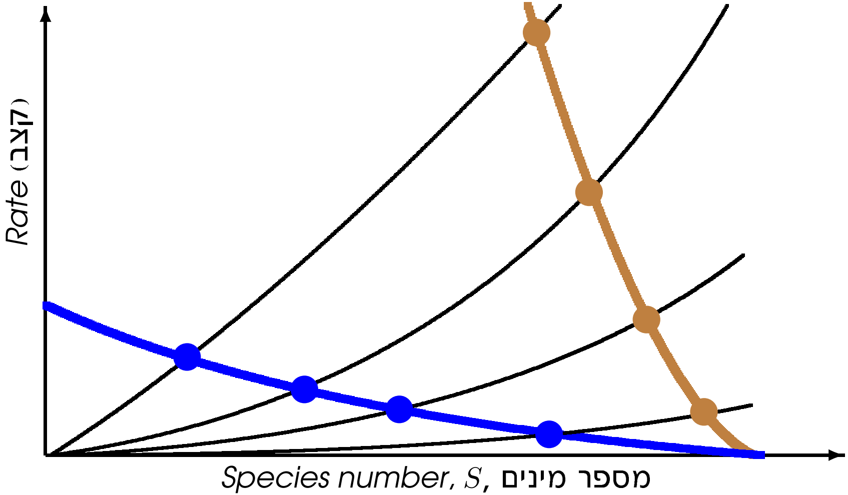
Application of TIB to species-area relations (SAR)

If the areas represent islands ⇒ low immigration rate, because isolation is high.



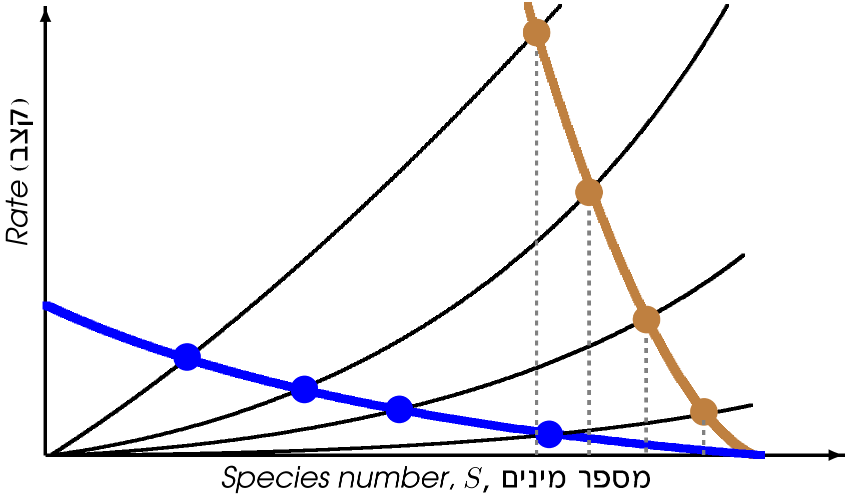
Application of TIB to species-area relations (SAR)

Species number at equilibrium increases with area; Turnover rate decreases with area.



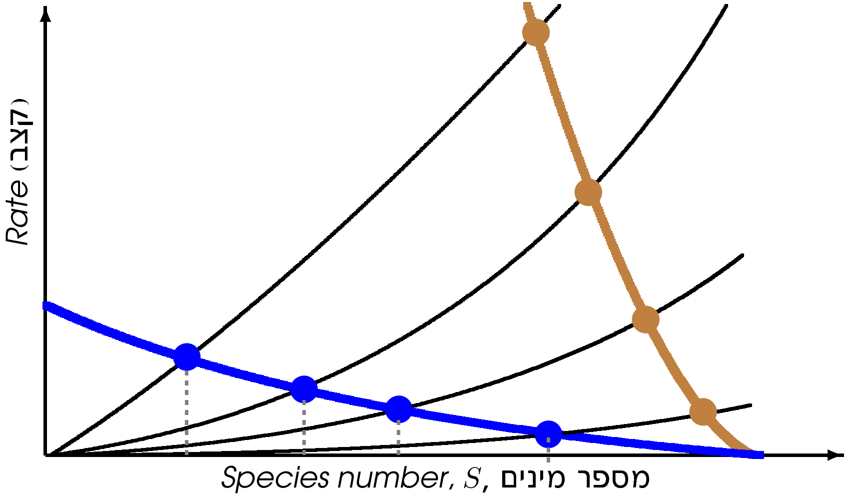
Application of TIB to species-area relations (SAR)

In continent, equilibrium species number declines slowly with decreasing area . . .



Application of TIB to species-area relations (SAR)

In comparison to the islands – where equilibrium species number declines faster as area decreases.



Application of TIB to species-area relations (SAR)

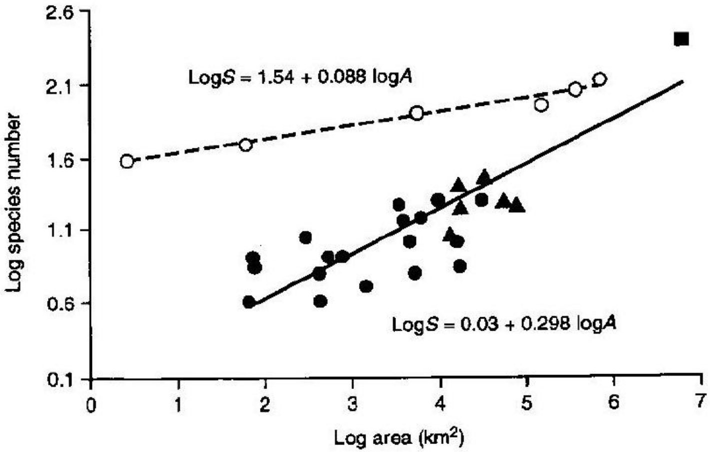
- This is exactly the pattern of species-area relation that we have observed when discussing species poverty on islands.

- Species-area curve for islands falls below that for areas within continents – representing species poverty.
  The island curve is also steeper – representing faster decline in species number with decreasing area.

Island area and species richness species-area curves

Ant species in New Guinea and Melanesia.

Mainland-island comaprison.



Application of TIB to species-area relations (SAR)

- This is exactly the pattern of species-area relation that we have observed when discussing species poverty on islands.
- Species-area curve for islands falls below that for areas within continents – representing species poverty. The island curve is also steeper – representing faster decline in species number with decreasing area.
- TIB provides predictions that fit to observed patterns of species poverty on islands.
- As well as species-area relations observed both within continents and in between-island comparisons.

Application of TIB to nature conservation

- A different application is related to conservation and planning of nature reserves within mainlands.
- Consider a natural area that is being partly destroyed because of human activities.
- For example, an area of sandy habitat is being partly built upon.

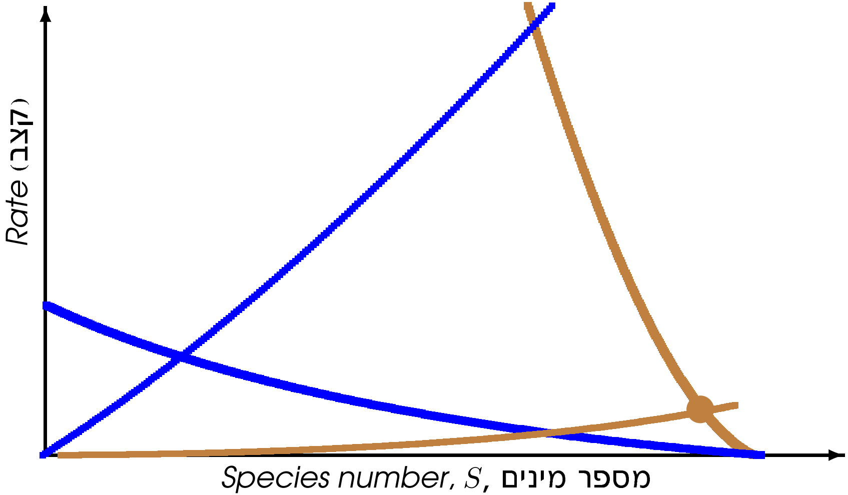
- The natural area is now smaller and also becomes more isolated from other such natural areas. In effect, it becomes a **“habitat island”**.

Application of TIB to nature conservation

Originally the area had high immigration rate and large area
⇒ Supports many species at equilibrium.

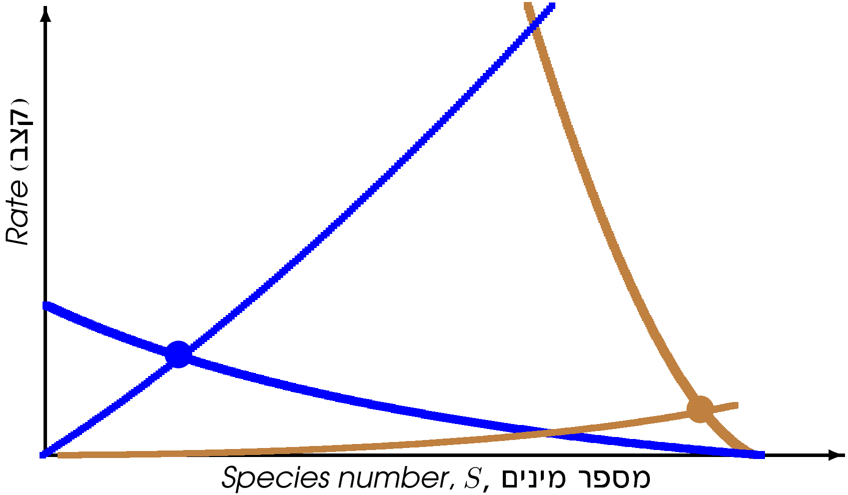
Application of TIB to nature conservation

After human activity, it becomes isolated and smaller – immigration falls, extinction rises.



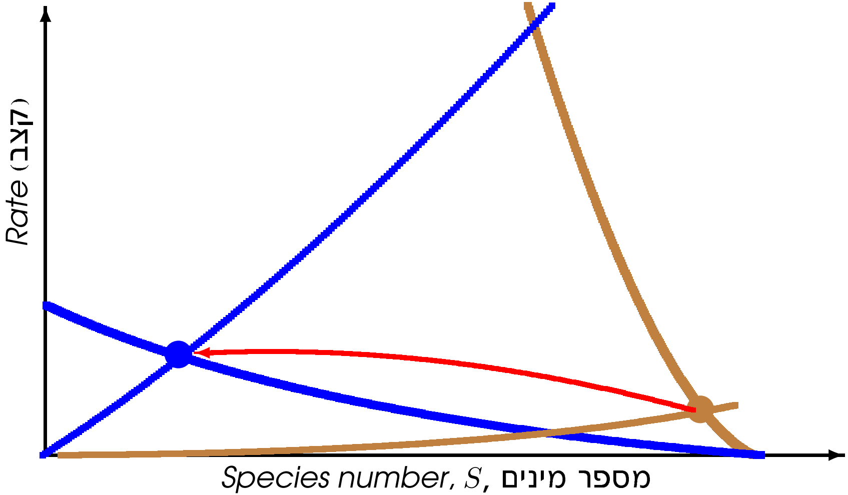
Application of TIB to nature conservation

New species number equilibrium .



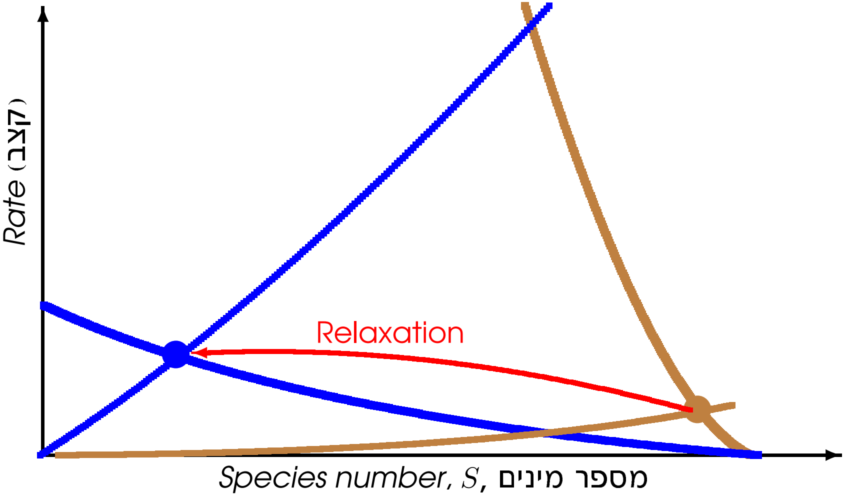
Application of TIB to nature conservation

Over time, the number of species will decline towards the new equilibrium point.



Application of TIB to nature conservation

A process called **Relaxation**.



Application of TIB to nature conservation

- According to TIB, when such human activities (or other destructive forces on natural habitats) act to diminish area and/or increase isolation, relaxation and loss of species is inevitable.
- However, with forethought and design, one can diminish the loss in biodiversity – for example, by designing "corridors" or an "archipelago" of such "habitat islands" so to diminish isolation and increase the effective area.
- Such applications have spurred much research into planning of nature reserves and land-use.

Summary of theory of island biogeography

- Was developed and applied originally to understanding the dynamics of biodiversity (species number) on continental islands – e.g., the Karakatau succession.
- Provides a mathematical and graphical model for effects of immigration and extinction ⇒ Provides predictions about equilibrium species number and turnover rates.
- Successfully applied to understanding SAR patterns in continents and in islands. But also to understanding biodiversity patterns within continents and to nature conservation – "habitat islands".
- This is yet another example of how island-related studies have lead to advances in ecology and evolutionary biology, in general.