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A qualitative model about the Island Biogeography theory

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Proposed by MacArthur and Wilson [1963; 1967], the Island Biogeography is a well established ecological theory used in the account of species diversity in communities. Within this theory, immigration and extinction are seen as the major driving forces in the introduction of new species from a source of colonizers (the ‘continent’) into a pool of species in the destination (the ‘island’). Immigration to the island is determined mainly by the distance of the colonizers source, so the more isolated is the island, the smaller is the immigration rate. Extinction is determined by the size of the island, so that smaller islands have smaller populations, more prone to local extinction. A central point of the theory, the insular equilibrium model, establishes that the number of species in an island is the result of a continuous disappearance of resident species (extinction) and replacement by new colonizing species (immigration).

A quite impressive amount of research was triggered by this theory (recent work includes [Fox and Srivastava, 2006; Kalmar and Currie, 2006; Heaney, 2007; Kadmon and Allouche, 2007]) but no qualitative models of the theory are published so far. This work presents a qualitative reasoning (QR) model [Weld and de Kleer, 1990] developed to support understanding of the most important aspects of the Island Biogeography theory. QR may be a useful approach because causal relations underlying the system are not explicitly demonstrated in mathematical models. Also the use of everyday language facilitates communication, making it easier for non-experts to understand the ecological concepts addressed by the theory. Given that this classic theory has been widely applied to management problems, it is important to have a qualitative model that could be used by students and decision makers, particularly those related to planning and management of protect areas, to learn, understand and make predictions about species diversity in different contexts. The model should be able to answer the following questions: (a) *what are the consequences of distance to the source and island area variation for species diversity?* (b) *How relevant processes influence species diversity?*

The model was implemented in the qualitative reasoning workbench Garp3 [Bredeweg *et al.*, 2006], using the ontology provided by the Qualitative Process theory [Forbus, 1984], particularly with respect to the use of direct influences and qualitative proportionalities to represent causal and mathematical relations. The system structure is modelled around the following entities: *Island*, *Community* and *Population*. These entities capture the notion that immigration and extinction processes operate at the level of the population, and species diversity is a feature of biological communities. Relevant properties of the entities are associated to quantities, and each quantity can assume qualitative values that represent possible states of the entity. The spatial reference for the phenomena described in the model is provided by *Island*, which is associated to the quantities *area* and *area growth rate*. *Community* is associated to the quantity *species diversity*, and holds a structural relation (‘contains’) with *Population*, which in turn ‘occupies the *Island*. The quantities *immigrants*, *emigrants*, *migration rate*, *speciation-extinction rate*, and *establishment-mortality rate* are associated to the entity *Population*.

The model library consists of 21 model fragments that encode descriptive aspects of the three entities and of the structural relations among them. Four processes drive the system dynamics in the model: area growth, migration, speciation-extinction, and establishment-mortality. In fact, they represent seven processes: *area growth* is related to changes in island area size; migration is a combination of *immigration* and *emigration*; *speciation* is the creation of new species, and this process is counter-balanced by *extinction*, the disappearance of existing species; finally, establishment-mortality is a combination of *establishment*, the survival of very young individuals in a particular environment, and *mortality*, their disappearance. All the four rates have quantity spaces {*minus*, *zero*, *plus*} so that the value *plus* is associated to positive effects of the processes (area increasing, immigration, speciation, establishment); *minus*, to the negative effects (area decreasing, emigration, extinction, mortality); and *zero* represents equilibrium between these effects.

The current version of the model has 20 scenarios for simulations that explore the effects of single and combined processes, as migration (to close and distant islands), migration combined to static and changing island areas, extinction and establishment of new species, until complex simulations involving all the entities and processes. The more complex simulation starts with the scenario ‘All the processes and area increasing’. Initial values of the quantities are as follows: *area growth rate* is *plus* and the rates of migration, speciation-extinction, and establishment-mortality are *zero*. The quantities *area, immigrant* and *emigrant* have value *medium*, and *species diversity* is *small*. This simulation produces one initial state and 109 states in total, from which 26 are end states that represent steady situations. The causal model and value history diagrams of relevant quantities are shown in Figure 1.

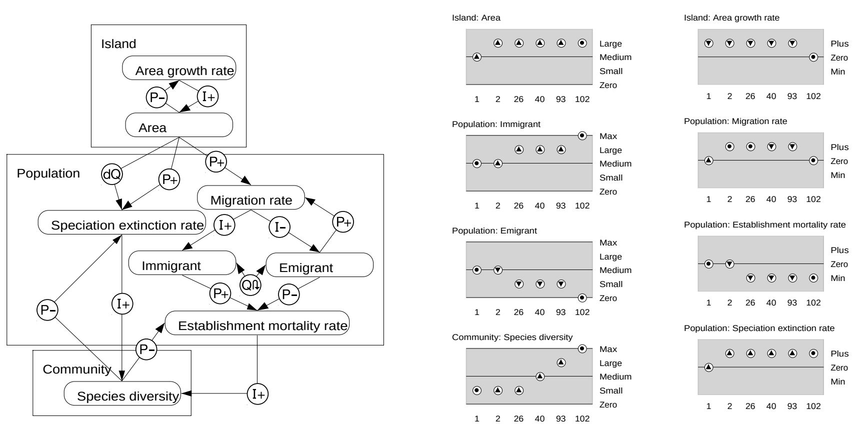

Figure 1. Causal model in state 1 and value history diagrams of relevant quantities.

In this simulation, causality flow starts with the area growth process. A feedback mechanism ensures that the area stabilizes at a certain point. While the area increases, for example, due to habitat regeneration, *migration rate* also increases. Once it assumes the value *plus, immigrant* increases and *emigrant* decreases. The inverse correspondence between these two quantities implements an assumption that keeps a close relation between them and reduces the number of states in the simulation. Changes in these two quantities propagate via qualitative proportionalities to *establishment-mortality rate.* This rate is also influenced by the derivative of *species diversity*. Without further information, this situation is ambiguous: the *rate* may increase (establishment prevails), decrease (mortality prevails) or remain stable, depending on the strength of the two influences. *Speciation-extinction rate* is influenced by changes in *area* and in *species diversity*, but it is assumed that the rate follows the derivative of *area* (see the correspondence between the two derivatives, *d_Q*), leading *speciation-extinction rate* to assume the value *plus*. The magnitude of *species diversity* is eventually determined by four processes: speciation, extinction, establishment and mortality, aggregated into two rates. The final outcome is not ambiguous, because although *speciation-extinction rate* and *establishment-mortality rate* are equal in state 1, from state 2 onwards speciation prevails and its rate becomes greater than *establishment-mortality rate*. As a consequence, *species diversity* increases, as shown in Figure 1. The behaviour path [1 →2 →26 →40 →93 →102] shows that *area* increases, *immigrant* increases and *emigrant* decreases; *migration rate* starts in zero, increases to *plus* and stabilizes and decreases until it reaches *zero* again. It is interesting to note all the quantities are stable in state 102: *area* is *large*, *immigrant* is *maximum* and *emigrant* is *zero*; *area growth rate* and *migration rate* are *zero*; *speciation rate* is *plus* and *mortality rate* is *minus*. *Species diversity* reaches the value *maximum*, and all the derivatives equal *zero*. This way, state 102 can be seen as an extreme case of insular equilibrium.

The model was able to answer the questions formulated above and produced interesting results. Explicit causal relations may be used to support predictions and explanations about the relations between distance to the source and island area to species diversity, and the model outputs are in accordance to the Island Biogeography theory. This way, distant islands are not colonized, and the bigger is the island, the smaller is the extinction rate and the bigger is species diversity.

However, during the implementation of the ideas developed in the theory some difficulties were found. It became clear that the mathematical model is far too aggregate as a knowledge representation of the ecological processes underlying the Island Biogeography theory. In fact, immigration and extinction alone cannot provide causal account for species diversity change. The solution implemented in the model was to include emigration and speciation and, for the sake of completeness, establishment and mortality (of young organisms), as species diversity does not increase only due to new species arrival, but because of they become well established. The current version is currently being extended in many aspects. For example, to create a better representation of the concept of 'isolated', by including the possibility of intermediate refuges between the source and the island, and to include the concept of 'habitat' in the model. In fact, this would scale up the theoretical coverage of the model, as recent studies are merging concepts from the original Island Biogeography theory and the niche theory to account for species diversity [Kadmon and Allouche**,** 2007]. Concluding, qualitative representations of ecological theories prove to be efficient to define the current understanding of causal relations and to make explicit hidden assumptions about the objects included in the model and to be clear about ecological processes involved in the dynamics of the system of interest. Using an everyday vocabulary to express these ideas has the potential to make ecological theories accessible to students and non-experts.

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