APPLICATION POSSIBILITIES OF GRAPH THEORY IN CONSERVATION

– Theses of PhD dissertation –

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2010.

1. Introduction, aims

Appreciation and support of conservation is constantly growing among people as well as among political actors, with the expectation of being as effective (with as low investments) as possible. To meet these expectations, there is a need for increasing objectivity during selection of species to protect. In addition to or instead of species that are traditionally popular, yet practically extinct in terms of ecological or evolutional perspectives, limited financial sources should be spent primarily on species having undoubtedly important role in maintaining ecosystem functions and services. Quantifying importance and so identifying presumed keystone species could result in a possibility for developing a long-term conservation strategy that is a prerequisite for effectiveness. Graph theory is an approach and methodological framework that provides an important tool for practical conservation.

We can benefit from the advantages raise from quantification not only in community ecological context. The idea can also be used in the field of landscape ecology: during the selection of important habitat patches or for monitoring certain changes; what is more, it may simplify the comparison of anticipated effects of different landscape management scenarios.

General aim

The general aim of my dissertation is to strengthen the approach that stresses the need for quantitative conservation. To do so I present diverse examples when graph theory may be applicable for conservation purposes; I start with mostly methodological issues and gradually move towards practice. I use different network types to demonstrate the suggested methods: first I focus on food webs then I deal with mutualistic webs, especially pollinator networks that are of great economic importance. Finally I present a case study on habitat networks.

On ecological networks

In community ecological networks, graph nodes usually correspond to populations of species. Graph links are specific relations, typically trophic interactions. The graph representation enables us to analyse indirect effects, such as trophic cascades that probably play a crucial role in the life of a community; nevertheless, their importance is not evident for the first sight. Hence, we can model secondary extinctions as well, and to predict the consequences of extinction of a certain species is a relevant issue in conservation.

Besides food webs increasing attention is paid to networks focusing on other interaction types. For example, pollination networks are special subwebs of an entire community, where links demonstrate mutually beneficial, “+/+” connections. It is also more and more common to examine networks modelling other ecology functions (e.g. plant-seed disperser, plant-ant or host-parasite webs).

From landscape ecological perspective, two different kinds of landscape elements are used. Graph nodes symbolize habitat patches; graph links represent ecological corridors connecting the patches.

Specific questions

1. Food webs

In network context probably species that hold a specific position within the web are more important in the life of the community than others. For instance they have many direct interactions (“neighbours”), or on the contrary: they are the link between species with many neighbours. These link species may ensure the integrity of the whole community. Nowadays many indices can be (or could be) used to assess the role of species within the community objectively – based on their position in the network. It is an interesting methodological question to explore the relationship of results derived from diverse approaches. In addition, this understanding can be fruitful for practice too, as different indices require different amount of input data, not to mention the fact that sensitivity of indices for network construction methods and mistakes varies a lot. Probably in most of the cases we should not make much more effort to use several indices to eliminate potential errors resulting from different sensitivity – especial if we know precisely whether or not we can expect something better or more with the application of a more complex index. Related to this topic, my specific questions are:

> **1.1.** To what extent do results overlap (produce similar ranking order of species) if we use distinct centrality indices reflecting different aspects of importance?
>
> **1.2.** Which indices give the most similar results to that of degree (number of direct neighbours), which the simplest and most commonly used index of positional importance of nodes in networks?

2. Pollinator networks

Similarly to trophic relations, interactions that affect plant reproduction (especially pollination) may have great importance in community life and assembly. Consequently, their analysis can help in better understanding of community functioning.

The need for protecting pollinator communities is emphasized by the fact that abundance of pollinator species is constantly declining due to their sensitivity for habitat fragmentation. In many cases the local declination of pollinators may result in less frequent pollination, which prevents plant species from reproduction; therefore the phenomenon is known also as "pollination crisis". As pollination is also an essential ecosystem service for mankind, the economic impact of the problem can be severe.

These mutualistic networks have a very characteristic feature, namely interactions are highly asymmetric, as usually plant species depend on animal species much more than vice versa. (Only some exceptions are known, like the obligate interaction that of between yucca and yucca moth). My questions are:

> **2.1.** To what extent can the asymmetric interaction pattern (the topology alone) ensure certain community functions – can a purely topological, binary index estimate the role of a species within a community?
>
> **2.2.** Will the rank of species alter if we set it based not only on the direct interaction patterns of species but in community context, regarding all the species at the same time?
>
> **2.3.** Can the community structure influence the development of a long-term conservation strategy?

3. Habitat networks

I present a case study to illustrate the possibilities of applying graph theory in landscape ecology. The analysis focuses on a bush-cricket *Pholidoptera transsylvanica* population in Aggtelek National Park, NE-Hungary living in some habitat patches connected with a number of ecological corridors. A key element in the long-term survival of this population is the maintenance of gene flow which can be assured by a well-connected habitat network. The site and the habitat network were examined in an earlier survey[1], where the relative importance of each landscape element was described. In this study the occurrence of the local population was re-mapped and the relative importance of every patch and corridor within the new habitat network was characterized. Comparison of the new rank of landscape elements with the earlier one may prove to be as an effective tool in the protection of the species as a good understanding of the processes that act on the field can serve as a basis for management decisions. My questions:

3.1. Have the structure of the habitat network and the relative importance of landscape elements changed during the decade between the two studies?

3.2. Is the change of the network topology or that of local population sizes the reason behind the changes of relative importances of landscape elements?

3.3. Concerning field conditions, how does creation of new ecological corridors or improvement of existing ones possibly influence the connectivity of the habitat network?

2. Methods

2.1. Food webs

I studied nine trophic networks of aquatic systems that describe carbon flows between trophic components. All of these networks were described in a methodically uniform way, therefore data sets are comparable. Furthermore, I analysed networks of similar size (they contain approximately the same number of trophic groups) in order to reduce the possible effects of size on the results. The indices to calculate were: degree, keystone index and its components, betwenness, information and closeness centrality, topological and weighted importance (concerning 1-10 steps).

Indices provide species ranks that can be classified irrespective of the fact that indices are based on precise values or they are sensitive only for the rank itself. A distance value can be defined based on correlations between pairs of indices for all the networks. These distances can then be clustered in order to produce a dendrogram for each community that displays the relationships of indices. A summarizing consensus dendrogram expresses the clusters that appeared in more than 50% of the competing results (i.e., at least in 5 dendrograms).

[1] Jordán, F., Báldi, A., Orci, K.M., Rácz, I., Varga, Z., 2003. Characterizing the importance of habitat patches and corridors in maintaining the landscape connectivity of a Pholidoptera transsylvanica (Orthoptera) metapopulation. Landscape Ecol. 18, 83–92.

Instead of presenting consensus dendrograms, there is another way to reflect between-index relationships for all networks at the same time: to unite all the nine data sets of the nine communities and do the clustering from this pooled data matrix. It has the advantage that minor details obscured by consensus generation may be revealed but the disadvantage is that webs with fewer nodes are underweighted.

2.2. Pollinator networks

First I used topological importance index to identify the topological constraints that act on the asymmetry of interactions. I used mutualistic networks from an international data base. Using Spearman rank correlation, I compared the resulting species rank with empirical asymmetry values based on field observations.[2]

In order to answer questions 2.2. and 2.3. I developed a new method to evaluate the role of species in community context, which regard all species in parallel. The model assumes that species are important if they transmit certain effects (by changes in their population sizes) towards the highest number of species, concerning indirect effects as well. The most important species are called topological keystone species as their importance is derived from their special position within the network topology. I used the KeyPlayer software developed in sociology to identify them. I considered two steps during simulations to take indirect interactions into account as well.

Then I looked for incrementally larger species sets (keystone species complexes) and determined their composite importance. I analysed whether or not larger complexes tend to contain smaller complexes, in other words, if complexes are nested. Additionally, I calculated the degree (describing the number of neighbouring nodes) of each species, which is a local index, viewing species on their own, and compared the degree based importance values with the above calculated results.

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[2] Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312 (5772), 431-433.

2.3. Habitat networks

As a first step in network construction, occupied habitat patches and ecological corridors connecting them were identified. Similarly to the preceding study, local population size served as a marker for patch quality, while an assessed permeability measure expressed the quality of corridors. Both landscape elements were evaluated on a semi-quantitative scale, ranging from 1 to 4.

For characterizing landscape elements I used both local indices describing only one node and more global indices concerning the topology of the whole network. In order to incorporate recent achievements of theory, I modified one of the indices and re-calculated the previous results and so I preserved the comparability of old and new findings. Some components of indices reflect network topology; some of them are related to local population sizes. By systematic variation of these components I could examine the effect of these factors per se.

During the second part of the survey, corridors that are relatively easy to create and others that could be improved were identified.. With these supplements I re-calculated the relative importance of landscape elements and evaluated the differences.

3. Theses

3.1. Food webs

3.1.1.a. There are no index pairs with completely the same performance. However, there is a robust pattern of how these indices are related to each other: some index pairs or groups in the dendrograms behave similarly; there are overlaps in the final ranks.

3.1.1.b. Based on the relationship of keystone indices, I conclude that indirect effects determine the importance and "keystoneness" of a species much more than direct interactions do. This fact has interesting implications for conservation applications.

3.1.1.c. However, based on the behaviour of topological and weighted importance indices, weighting is a more important aspect during classification than the number of steps. It suggests that the number of steps has a smaller role than we could conclude from the analysis of keystone indices (3.1.1.b.).

3.1.2. If the network is unweighted, betwenness and information centrality are suitable measures of positional importance. They give more precise estimations than either degree or closeness centrality as results derived from *BC* and *IC* are closer to that of weighted indices. This information might be useful for practice as undirected networks are probably more readily available, since registering the topology itself without link weights is easier to implement.

3.2. Pollinator networks

3.2.1. Within a mutualistic community, especially in case of pollinator networks, topology per se estimates the results based on accurate field data remarkably well. This suggests that community structure determines the processes related to the asymmetric interaction configuration to a great extent.

3.2.2. If we have a good knowledge about species and their relations, the newly developed method may be appropriate for selecting the most important species in a way that regards the community as a whole. Multispecies focus should be prevalent as comprehension of a species' importance may change fundamentally compared to the case when we grab species out of the community context. The reason behind is that a highly local focus can not consider species having only a few interactions – but acting as a bridge and thus maintaining the integrity of the community.

3.2.3. Conservation may be more effective if the most important species is part of the species complex containing the two most important species, which is incorporated into the set of the three most important species (in other words, if species complexes are nested). Otherwise, protection of "proper" species (that is currently the best for the whole community) is a function of financial sources. This may make the development of a long-term strategy more difficult.

3. Habitat networks

3.3.1. Excessive recent fragmentation of the network poses a great threat for gene flow hence long term survival of the species. Patch N5 (*"Nagy Nyilas"*) and the connecting link L5-18 have major role in maintaining connectivity.

3.3.2. Change in topology alters the network structure more than change in local population sizes; however, it is not the reason behind the recorded variation per se. From a practical viewpoint it means that preservation of the network structure is crucial during species conservation.

3.3.3. Establishment of new corridors probably has no significant effect; improvement of existing corridors or preventing them from being destroyed is most likely to be effective (and easier to implement in the field).

4. Conclusions

Application of computable, objective and predictive methods is a more and more compelling urge in conservation practice. My dissertation displays that graph theory can be an exceedingly useful approach for such purposes, due to its quantitative feature (its potential for selecting items objectively). What is more, it can indicate the relation between community structure, community dynamics and ecosystem functions and also between community conservation and species or area protection achievable in practice.

5. Publications

Benedek; Zs., Jordán, F., Báldi, A., 2007. Topological keystone species complexes in ecological interaction networks. *Community Ecology*, 8 (1), 1-7.

Jordán, F., Benedek, Zs., Podani, J., 2007. Quantifying positional importance in food webs: A comparison of centrality indices. *Ecological Modelling*, 205 (1-2), 270-275.

Benedek Zs., Jordán, F. és Báldi, A. 2007. Kulcsfajkomplexek kutatása és ennek alkalmazási perspektívái a természetvédelem hatékonyságának növelésében. *Természetvédelmi Közlemények*, 13: 27-36.

Benedek, Zs., Nagy, A., Rácz, I.A., Jordán, F. és Varga, Z. 2009. Az erdélyi avarszöcske (Pholidoptera transsylvanica, Fischer Waldheim, 1853) élőhelyhálózatának változásai az Aggteleki karszton. *Természetvédelmi Közlemények*, 15: 369-380.

In preparation:

Benedek, Zs. Nagy, A., Rácz, I.A., Jordán, F., Varga, Z., Landscape metrics as indicators: quantifying habitat network changes of a bush-cricket Pholidoptera transsylvanica in Hungary. *Ecological Indicators*, under revision.

Kahramanogullari, O., Jordán, F., Benedek, Zs.: CoSBiLab LIME: a software for building stochastic dynamical ecosystem models. *In preparation.*

Further publications on the topic of dissertation

Conference participations

Benedek, Zs., Nagy, A., Rácz, I.A., Jordán, F., Varga, Z. Network-based methods in landscape management - Changes in the habitat network of Pholidoptera transsylvanica (Fischer Waldheim, 1853) in the Aggtelek Karst, Hungary. Poster, 2nd European Congress of Conservation Biology, Prague, Czech Republic, 2009. Book of abstracts, pp. 155.

Benedek, Zs., Gallasi, K., Jordán, F. Asymmetric interactions in plant-mutualistic networks. Structure and function. Lecture, EURECO-GFÖ, Leipzig, Germany, 2008. Proceedings, pp. 465.

Benedek, Zs., Gallasi, K., Jordán, F. *Aszimmetrikus kapcsolatok növény-mutualista hálózatokban: szerkezet és funkció*. Lecture, 3. Quantitative Ecological Symposium, Budapest, 2008.

Benedek, Zs., Nagy, A., Rácz, I.A., Jordán, F., Varga, Z. *Az erdélyi kurtaszárnyú szöcske (Pholidoptera transsylvanica) élőhelyhálózatában beállt változások nyomon követése és a további változások hatásainak becslése.* Poster, 5. Hungarian Conference of Conservation Biology, 2008. Book of abstracts, pp. 83.

Benedek, Zs. Network analysis in conservation practice. Lecture, International Life Sciences Students' Conference, Ljubljana, Slovenia, 2007.

Benedek Zs., Jordán, F., Báldi, A. The network architecture and nestedness of topological keystone species complexes in plant-pollinator communities. Poster, 1st European Congress of Conservation Biology, Eger, 2006. Book of abstracts, pp. 395.

Benedek Zs., Jordán, F., Báldi, *A. Kulcsfajkomplexek és a természetvédelem hatékonysága*. Poster, 3. Hungarian Conference of Conservation Biology, Eger, 2005. . Book of abstracts, pp. 94.

Popular writings

Benedek, Zs. 2008. Beporzók veszélyben. *Természet Világa*, 139 (5), 201-203.

Benedek, Zs., Vasas, V., 2008. Az útépítés útvesztőjében. Az élőhelyek feldarabolódása és a biológiai sokféleség. *Természet Világa,* 139 (10), 454-456.