Predicting biological invasions
Development and application of a model for the analysis of plant invasions
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Summary

The prediction of invasion processes brings along an array of difficulties. The aim of this study is to analyze these difficulties, thus contributing to the answer of the question: "Can we predict biological invasions?". This question can only be answered on the basis of a detailed analysis of the invasion process. For this reason, as a first step a model is developed, which from an organism-centered perspective determines the main factors influencing processes of plant invasion.

The principle of the model is a dissection of an idealized invasion process into invasion steps and stages (INVASS model). The basic structure can be depicted as a staircase: five invasion stages (0 to 4) are connected through four invasion steps (1 to 4). The stages describe the status of the species during the invasion, whereas the steps illustrate the processes. The invasion steps summarize the main difficulties the species may be confronted with during the process.

The fine structure of the model consists in a detailed analysis of the four steps of invasion. For each step the problems are named the invading species may be confronted with. Additionally, species characteristics are listed which increase the probability that the potential problems can be avoided or solved. And, at last, favorable conditions of the new environment or during transportation are identified, which may as well increase the probability of invasion success. The potential problems, favorable species characteristics and other favorable conditions are summarized in four tables.

The model is applied to the example of South African Ragwort (*Senecio inaequidens*) spreading in Europe. It becomes clear that during each invasions step in this case - as the model hypothesizes - various problems occurred, and each of them has been overcome with the help of step-specific characteristics or environmental conditions. Thus, the INVASS model proves to be a useful basis for a detailed description and explanation of single invasion
cases. With the help of the model, available knowledge can be summarized in a systematic way, and gaps of knowledge become apparent.

Concluding the results up to this point it has to be emphasized that there are not just a few key factors determining processes of biological invasions. The course of a specific invasion rather is determined by the contingency of situations. The result of an invasion process thus depends on the history of the sequence of events (historicity). It is shown that taking into account the influences of contingency and historicity makes it possible to give a new impetus to some disputed question about the importance of certain factors for the course of an invasion process.

Socioeconomic factors can have decisive influence on the progress of an invasion. This is another subject where the INVASS model proves useful as a heuristic basis for investigations: the various possibilities how socioculturally determined actions may influence processes of plant invasion can be summarized in a detailed and systematic way.

On the basis of the model the question is discussed to which degree biological invasions are predictable. The possibilities to predict which plant species will establish in a certain area are limited due to different circumstances:

- The complexity of the process, i.e. the huge amount of heterogeneous and potentially interacting factors, leads to a methodical limitation of predictability.
- The strong influence of historicity and the contingency of events in most cases delimits the possibilities of prediction to statements of vague probabilities.
- As a consequence of the 'base-rate-effect', invasion events which are relatively unlikely can only be predicted on the basis of quite accurate models.
- Ecological foreignness of the invading species in the new area brings along further limitations to predictability, which can be moderated to some extent with increasing accuracy of the underlying models.
- Genetic processes (above all genetic drift) can have principally unpredictable effects on biological invasions.
- At last, the influence of socioeconomic factors in some cases makes it impossible to make predictions based on the methods of natural sciences alone. It is discussed what difficulties arise for prediction if intentional actions influence an invasion process.
The INVASS model is suitable to improve the possibilities of prediction, because it moderates some of the named problems. Principal limitations due to ecological foreignness, genetic effects and the influence of socioeconomic factors nevertheless remain.

Finally it is shown how the INVASS model may be integrated into existing approaches for risk assessment. It becomes apparent that from a theoretical point of view the four tables can be a valuable tool for the assessment of the invasiveness of plants. Further research should prove the applicability of the model in this context.

The PhD thesis is published in German with the title "Zur Vorhersagbarkeit biologischer Invasionen. Entwicklung und Anwendung eines Modells zur Analyse der Invasion gebietsfremder Pflanzen" in Neobiota 4 (2004), Berlin, for 20 € available from t.heger@wzw.tum.de