

**Posudek disertační práce Pavla Fibicha:  
The effect of neighbours in plant communities: mathematical and  
experimental approaches**

Předkládaná práce sestává z šesti článků, napsaných na velice dobré úrovni. Tři z nich jsou publikovány ve velice dobrých časopisech: Folia Geobotanica, Ecological Modelling, Journal of Plant Ecology, čtvrtý pravděpodobně vyjde v Journal of Vegetation Science, což samo o sobě dostatečně vypovídá o kvalitě této práce. Další článek je odeslán do tisku a jeden je prezentován jako manuskript.

Autor se ve své práci zabývá vlivem okolních rostlin na hemiparazitické druhy, otázkami produktivity vs. diverzity, celkovou finální produkcí biomasy a uchycováním juvenilních rostlin. Metodicky jde o kombinaci modelového přístupu pomocí diferenciálních rovnic a modelů populací založených na chování jednotlivých příslušníků populace s alespoň částečnou experimentální verifikací výsledků ve skleníkových a terénních experimentech.

Dizertace je opatřena úvodem, který stručným a jasným způsobem uvádí čtenáře do problematiky, a závěrečnou diskusí, v níž jsou dosažené výsledky dány do kontextu s výsledky jiných autorů. I zde je sympatický koncizní styl doktoranda.

Sám fakt, že tři z šesti předkládaných článků prošly tvrdou recenzí v prestižních časopisech naznačuje, že je těžké těmto článkům nyní něco dalšího vytknout. Zbylé tři jsou dle mého názoru též velice dobré úrovně. Matematické výsledky, které jsem byl na základě dizertace schopen ověřit, jsou dle mého názoru technicky správné a bez chyb. Spíše zde proto uvádím jednu myšlenku, která s předkládanou prací souvisí a již by bylo v diskusí při obhajobě vhodné věnovat nějaký čas, čímž by též kandidát prokázal mimo jiné i své schopnosti vědecké disputace. Jde o tuto otázku:

Rostliny jsou sedentárními organismy, zatímco systémy diferenciálních rovnic použité třeba v článku 1 předpokládají, že zde interaguje „každý s každým“. Do jaké míry a za jakých podmínek může tento fakt ovlivnit v článku dosažené výsledky?

K práci mám drobné stylistické poznámky:

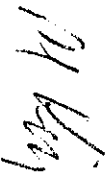
- a. Str. 26, popiska obr. 2.6: „relevs“ je asi překlep, správně by mělo být „relevés“?
- b. Str. 40 a dále: „according to“ spíše než „according“
- c. Str. 40: „logistic growth“ spíše než „logistic grow“.
- d. Str. 40 a dále: preferoval bych „ $b_{max}$ “ před „ $b^{max}$ “, protože druhý výraz implikuje exponent. Podobně u „ $f_{min}$ “ dále.
- e. Str. 66, Table 4.1.: „Growth rate“ spíše než „Grow rate“.
- f. Str. 74 – vynechat závorku před „Kotorová“.
- g. Str. 83 – asi spíše „Fox's“ než „Foxs“.
- h. Pokud je více rovnic pod sebou, preferoval bych mezi nimi větší mezery – takto písmenka často splývají a text je proto těžko čitelný.

Jak jsem již zmínil výše, má otázka je miněna spíše pro povbuzení diskuse, v žádném případě nesnižuje vědeckou kvalitu předkládané práce. Kritizované překlepy jsou též malíčkosťmi.

Z autorovy publikační činnosti, vysoce nadprůměrné pro doktorského studenta, proto zcela jednoznačně vyplývá, že Pavel Fibich prokázal během svého doktorského studia schopnost samostatně vědecky pracovat a publikačně zpracovat získané empirické poznatky.

**Závěr:** Pavel Fibich jednoznačně prokázal schopnost samostatné vědecké práce a splnil veškeré požadavky kladené na doktorandské studium. Jednoznačně doporučuji přijetí jeho disertační práce k obhajobě.

Rennes, 16. října 2012



Prof. RNDr. Pavel Kindlmann, Dr.Sc.

Review of Pavel Fibich's Doctoral Thesis 'The effects of neighbours in plant communities: mathematical and experimental approaches'

**Reviewer: Peter Stoll, University of Basel**

The thesis of Mr Pavel Fibich consists of six articles, three of which have been published in international, per-reviewed Journals. Pavel Fibich is the first author of two of them published in *Folia Geobotanica* and *Ecological Modelling*. He substantially contributed to the third one published in *Journal of Plant Ecology*. A fourth one with Pavel as first author appears to have been accepted by *Journal of Vegetation Science*. From the remaining two manuscripts, both with Pavel as first author, one is submitted. The six articles are preceded by a general introduction and followed by a general discussion. Overall, the published papers are of high quality and the manuscripts have the potential to eventually be published in international, per-reviewed Journals. The thesis clearly demonstrates Pavel Fibich's talents and abilities in mathematical modeling and experimentation needed to independently conduct successful ecological research.

In the **General Introduction** (Chapter 1), Pavel gives an overview of his thesis and its different parts putting them into the relevant context of spatial patterns, biodiversity experiments and mathematical methods. For example he concisely and competently summarises the important differences between top-down mean-field models and bottom-up individual based models.

In **Paper 1** (Chapter 2) a mean-field model for the root hemiparasite – host plant interaction emphasising productivity gradients and above ground competition for light is proposed and analysed. The model demonstrates that hemiparasites have no chance to persist at very low productivities because there are too few poor hosts. At the other end at high productivity, hemiparasites are outcompeted by their hosts leading to eventual extinction of the hemiparasites. At intermediate productivities, hosts and hemiparasites may coexist but the coexistence is not always stable and includes unstable, possibly cycling dynamics. Competition for light is essential in explaining these patterns and a comparison with field data suggests that the model indeed captures the pattern of declining proportion of hemiparasitic plant species with increasing productivity as *Mathies* conjectured. All in all a nice modelling exercise that consequently extends previous incomplete models by adding biologically relevant mechanisms.

The connection of Paper 1 with the other chapters in Pavels thesis is somewhat obscure. In other words, Paper 1 is somewhat isolated.

In **Paper 2** (Chapter 3), an individual based and spatially explicit model (IBM) is proposed and analysed in the context of recent experimental studies showing that more diverse plant communities have higher productivity. Experimentalists developed biodiversity indices and used them to quantify effects such as overyielding, complementarity and selectivity. Moreover, these indices have been claimed to capture the main mechanisms (e.g. complementarity) that lead to increased yields. To test and critically evaluate these claims, Pavel developed and used a spatially explicit and individual based model and compared the behaviour of selected biodiversity indices with expectations based on life history traits of constituent species. More specific, he used increasing size variability to drive a selection effect or increased shade tolerance of the smaller species to increase complementarity. Both scenarios lead to the expected behaviour of diversity indices. However, shortening the length of stress tolerance of the weaker species increased diversity indices whereas a decrease would have been expected. Varying sowing density and spatial pattern revealed that effects of density were more pronounced than effects of spatial pattern. This is important to know because experiments often ignore possible density effects. In particular at high densities where yield of constituent species may decrease (rather than staying constant), important interactions happened at early stages of mixture development leading to counter-intuitive behaviour of indices.

I very much liked the critical discussion of this contribution emphasizing possible

shortcomings of both modelling and experimental approaches. Pavel and collaborators themselves were motivated by their simulations results to test effects of sowing density on biodiversity indices and their interpretation (see Paper 3 below) and this, I believe, should be attempted more often in future research because all too often modelling or experiments are carried out in isolation from each other. In this respect, I would have very much appreciated a closer integration of the model with the experimental test.

#### **Manuscript 1 (Chapter 4)**

Having shown that constant final yield (CFY) is an important conceptual ingredient in biodiversity indices (see papers 2 & 3), Pavel and co-authors present a field of neighbourhood model to investigate the role of spatial pattern, individual variability and mortality for CFY. Their main result emphasises that individual variation is important for population processes. Hence, CFY is more unlikely or even 'violated' in homogeneous populations with uniform sowing patterns such as plantations. I would like to highlight plasticity of plants as aspect of the model which I believe to be important yet neglected in many other models. In their model, plasticity was included by allowing plants to increase height growth under strong competition. But then, they somehow miss the opportunity to investigate effects of varying plasticity on biomass density relationships.

In **Paper 3** (Chapter 5), Pavel and co-authors report on the results from a biodiversity experiment with varying density and show that biodiversity effects are affected by density. In particular, the yields of both monocultures and mixtures were influenced by density. This is an important finding because it is usually assumed that biomass density relationships lead to constant final yield (CFY) which builds the basis for calculations of biodiversity effects. But the results presented in paper 3 (and the modelling results presented in paper 2 above) show that this may not necessarily be assumed or be empirically supported. As a consequence, net biodiversity effect, complementarity and selection effect increased with density. Thus the main conclusion that the shape of the density-productivity curve is fundamental for the behaviour and interpretation of biodiversity effects may be judged as important contribution to plant ecology. In his thesis, Pavel presents evidence from both theoretical modelling and experimental data to support this conclusion.

In **Manuscript 2** (Chapter 6), Pavel and co-authors compare different methods to analyse biodiversity effects using the data presented in paper 3. Although ecological interpretations from the three methods they compared were similar in many respects, they conclude that additive partitioning should be preferred because it provides better insights into mechanisms than the linear-model-based methods. The disadvantage of additive methods on the other hand is that it has much higher requirements for data collection because if monoculture performances of all species must be present and contributions of all species to all mixtures must be known. Obviously, this is not feasible in experiments with many species or even impossible for specific ecosystem functions such as respiration. On the other hand, it explains why this approach yields more informative insights.

While I liked the methodological approach of this chapter and its concise and informative introduction, I found the presentation of the results difficult to follow but this has also to do with the complex nature of the different methods. I wondered, however, why the simulated data from paper 2 were not included in this methodological comparison. Perhaps this would have lead to a more direct demonstration of the essential differences in the three methods. Reassuring was the fact that all three methods concordantly demonstrated that the ecological interpretation of the results depended on the sowing density.

In **Manuscript 3** (Chapter 7) the establishment of recruits in meadow gaps was investigated in an experiment with or without sterilized soil to manipulate the seed bank. A second treatment, inserting mesh or felting along the gap borders was used to enable or disable clonal spreading. Not surprisingly, the presence of a seed bank enabled earlier gap colonization and the effect of the seed

rain became increasingly important during the season. Perhaps a bit surprising was the fact that clonal spreading in general was far less common than recruit establishment from seeds which emerged initially close to the gap centre. Later, recruits from seeds preferred the southern more cooler part of the gaps. This shift in preferred location was interpreted as showing a shift to increasing importance of facilitative effects (less transpiration and hence better water status) of the surrounding vegetation. This interpretation could be easily challenged because the pattern of shifting recruitment form centre to border of gaps could simply be due to already occupied gap centres.

In the **General discussion** (Chapter 8), the topics of the previous chapters are concisely summarized. One of the main conclusion that the shape of the density-productivity curve is fundamental for the behaviour and interpretation of biodiversity effects may be judged as important contribution to plant ecology. In his thesis, in particular chapter 3 & 5, Pavel presents evidence from both theoretical modelling and experimental data to support this important conclusion. Chapter 4 builds the theoretical fundament connected to chapters 3 & 5 because it investigates CFY with the help of a sophisticated simulation model. In chapter 6, methods to analyse diversity experiments were compared. I wondered, however, why the simulated data were not included in this comparison. Chapters 2 and 7 are somewhat disconnected from the overall topic of biodiversity effects. Nevertheless, particularly the model in chapter 2 but also the experimental approach used in chapter 7 clearly demonstrate Pavel Fibich's talents and abilities needed to conduct successful ecological research. Speaking as a reviewer for many journals, I expect the remaining manuscripts to be published in good, and sometimes pre-eminent, scientific journals in due course.

In conclusion, I have no hesitation in recommending this work for the award of the PhD qualification. The thesis provides a body of work that is a good example of how much theoretical and experimental work in ecology can contribute to the field when it is well thought out, conducted, analysed and interpreted. The novel results will not only serve as valuable tests of existing hypotheses but should also go on to inspire new work in ecology both experimental and theoretical.

Yours sincerely,

Basel, 14. October

Peter Stoll

