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Biogeography of artificial islands: effects of age, area, elevation, and isolation on plant species richness

Biogeografie umělých ostrovů: vliv stáří, plochy, převýšení a izolace na druhové bohatství rostlin

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Dedicated to the memory of Slavomil Hejný

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Vascular flora of 71 artificial islands of varying age was analyzed in 22 fishponds, Třeboň Basin, the Czech Republic. Data on species richness were interpreted in terms of Wilson's (1969) hypothesis on the development of biotic communities. An increase in species richness during the non-interactive stage (one to two years) and a decrease in the interactive stage (three to six years) were both statistically significant. As predicted, by Wilson's hypothesis, there was also an increase in species richness in the assortative stage (seven to >50 years), however, this trend was not significant. This successional pattern was confirmed by the vegetation development recorded on 34 re-sampled islands. For these islands the positive change in species richness during the assortative stage was significant based on both paired t- and binomial tests. Contributions of island area, elevation, and isolation during individual successional stages were evaluated. As a whole, this is probably the first clear confirmation of Wilson's hypothesis for vascular plant communities on islands.

Keywords: Assortative stage, colonization, fishponds, interactive stage, non-interactive stage, Třeboň Basin, succession, Wilson's hypothesis

Introduction

Successional changes in species diversity belong to frequently discussed topics in contemporary ecology (Dajoz 1996, Molles 2002). Reported trends range from simple statements about monotonic increase of species richness during succession (Mellinger & McNaughton 1975, Miles 1979, Slavíková 1986), to rather sophisticated descriptions of more complicated patterns (Whittaker 1975, Peet 1978, Prach 1987, Rejmánek & Rosén 1992, Lichter 1998). In the context of island biogeography, Wilson (1969) postulated four stages (dynamic equilibria) of the organization of a biotic community: noninteractive, interactive, assortative, and evolutionary. Noninteractive conditions exist when abundances of species are too low to cause competition for resources that would lead to species exclusion. Interactive 'equilibrium' results when competition causes local extinction of some species. In the assortative phase species are sorted in such a way that more of them can be packed in the community. Finally, coevolution of species allows total exploitation of resources to become even more efficient, resulting in a further increase in the number of coexisting species. Only the first three stages are usually considered in field studies of colonization/succession (Rejmánek 1983). Wilson's hypothesis was addressed in experimental and observational studies on communities of arthropods (Mackay 1993, Simberloff & Wilson 1970), corals (Grigg &

Maragos 1974, Loya 1976), soil hyphomycetes (Wildman 1987), and phytobenthic communities on glass slides (Cattaneo et al. 1975), as well as in microcosm experiments (Dickenson & Robinson 1985, Have 1987, McCormick & Cairns 1992). Some studies of vegetation succession can be interpreted in terms of Wilson's hypotheses as well (Reiners et al. 1971, Peet 1978, Schmidt 1981, Monk 1983, Prach 1987, Osbornová et al. 1990, del Moral 1999, Chytrý et al. 2001). Surprisingly, however, relevant data on colonization of new islands by plants seem to be scarce for both natural and artificial islands (Whittaker et al. 1989, Shaffer et al. 1992, Odland 1997, Harrison et al. 2001).

This study aims to describe and explain changes in species richness during colonization/succession of artificial islands in fishponds. The fishponds are located in Třeboň Basin, South Bohemia, the Czech Republic. Třeboň Basin is a flat or slightly undulating region near the Austrian border in South Bohemia. Six centuries ago the swampy area of the basin was drained by a complicated network of channels, and an extensive system of fishponds was created. These fishponds (shallow artificial lakes) range from one to > 400 ha in area and their average and maximum depth rarely exceeds 1.5 and 4 m respectively (Hejný & Květ 1978). In several of these fishponds there are islands as old as the ponds themselves; we regard those as “natural” and most similar to the “climax” communities. In addition to these relatively few natural islands, hundreds of artificial islands have been created in the fishponds as a regular part of their modern intensive management (Hejný & Husák 1978). Every 10 to 20 years, the fishponds are drained and dradged sediments are piled up to form islands. The main purpose of this activity is to remove rooted perennial plant communities from shallow littoral zones in order to increase the open water area and to prevent the terrestrialization of the ponds (Hejný & Husák 1978). The artificial islands range in size from a few square meters to 2000 m^2.

The succession on these islands can be classified as a secondary succession. However, it is a rather special type of secondary succession because the original communities and substrates were destroyed several hundreds of years ago when the fishponds were created. Substrate of the artificial islands consists mostly of recent fishpond sediments rich in organic material.

The presence of islands of various ages, sizes, and distances from the shore provides an ideal system to address some basic questions of island biogeography. We therefore asked: (1) Can Wilson’s stages be recognized in this system? (2) If so, how is the species richness in particular stages related to island area, elevation, and isolation.

Methods

Study site

The study area is located in Třeboň Basin, South Bohemia (49°05'N, 14°48'E; altitude 380–460 m). Vegetation on 71 islands in 22 fishponds was analyzed (Table 1). The major criteria for selection of individual islands were their accessibility and equal representation of different age categories. Also, we avoided islands of heterogeneous origin, e.g., islands expanded in the course of repeated dredging. As a result, about 50% of artificial islands available in Třeboň Basin in the early 80’s were sampled. Five islands were selected as ‘climax’ communities. Vegetation on these five islands was similar to mature forest communities reported for the Basin (Březina 1975). Resident trees were definitely > 50 years old judging from their dbh.

Table 1. – Location, age, and area of 71 analyzed islands.

Fishpond name	Island age (years)/area (m^2)
Černíš	5/604, 5/1130
Dobrá vůle	3/707**
Farský	4/4, 4/43, 4/118, 4/251
Humlenský	2/196, 2/211, 2/212, 2/253, 2/540, 2/706
Krajina	1/9, 1/9, 1/12, 4/408**, 4/2355**, >50/282
Kuvinský	2/2**, 2/6**
Láska	14/66**, 14/69**
Lipičí	4/326**, 15/126**
Měkký	1/235*, 1/565*, 1/424
Naděje	14/13**, 14/224**, 25/260**, 25/942**, 25/989**, 25/1164, 25/1960, 25/1969
Nový u Frahelže	20/5, 20/47
Okřínek	19/236**, 19/942**
Ostrý	19/308**
Pasecký	9/47**, 9/134**, 11/236
Perklas	>50/550, >50/1295
Ponědrážský	>50/7850
Pražák	4/4**, 4/5**, 4/9**, 4/11**, 4/35**, 4/188**, 4/565, 4/848, 4/1590
Skutek	5/118, 5/236, 5/275, 5/424
Starý vdovec	2/245**, 2/659**, 2/2414**
Strakatý	1/31*, 1/754*, 1/14, 1/165
Velký rybník	14/259**, 14/990, >50/1276
Víra	14/236**

*Resampled after 1 year. **Resampled after 2 years.

Data collection

For each island we found the age from the records of the Fisheries Department (Státní Rybářství) in Třeboň. We estimated the area of an island as an area of ellipse based on two perpendicular measurements approximating major and minor axes. The island elevation was measured as an elevation of the highest point above the water level. The isolation was measured as a distance to the nearest point on the pond shore. A complete list of species was compiled for 71 islands. The data were recorded in 1981, 1982 and 1983. A subset of 34 islands was re-sampled after one or two years (Table 1).

Data analysis

Preliminary examination of the data revealed a substantial increase of the species number between the 1st and 2nd year, decrease in subsequent years, and a slight increase of species richness on the oldest islands. Based on this finding, we summarized the records of species richness into five time intervals: 1st year, 2nd year, years 3 to 6, years 7 to 25, and “climax” islands (> 50 years).

In terms of R^2, regressions of the number of species (S) on log(area) were, in general, better than regressions of log(S) on log(area). Because of the strong linear species-log(area) relationship in all five age categories ($R^2 = 0.874$, 0.746, 0.713, 0.636, and 0.817, respectively), means of standardized species numbers, calculated as S/log(area), were used for comparisons of the successional stages (Fig. 1).

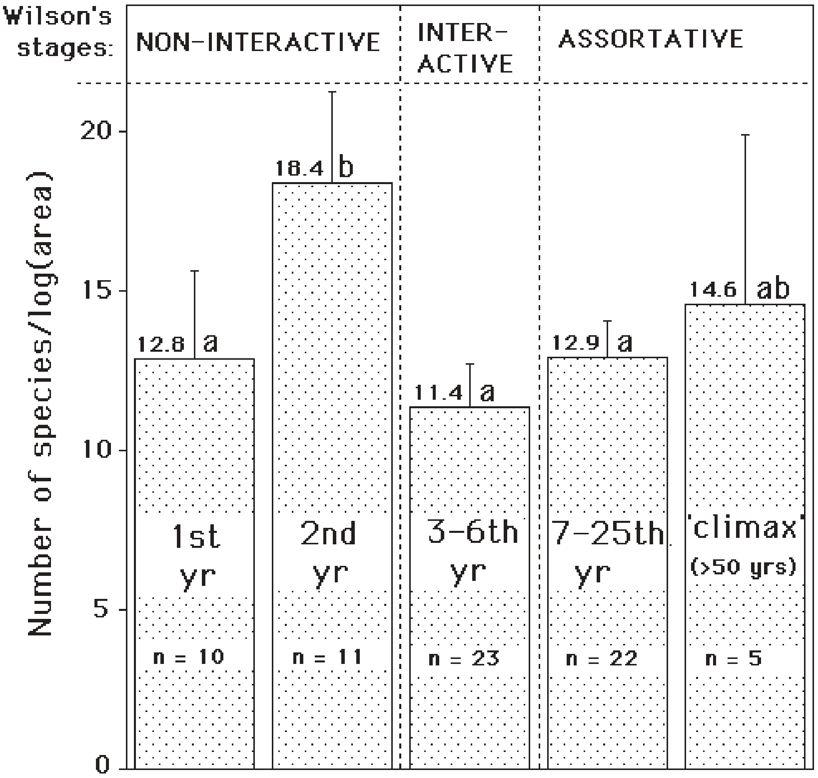

Fig. 1. – Changes in species richness of vascular plants on islands of different age interpreted in terms of Wilson's stages of community development. Species richness (S) is standardized by $\log_{10}(\text{area}[m^2])$. In effect, this is an estimate of the number of species growing in 10 m^2. Means for age groups sharing the same letter are not significantly different (Scheffé test, p = 0.05). Vertical bars represent standard deviations.

Multiple comparison of means was conducted by Scheffé test (Hsu 1996). Changes in species richness on re-sampled islands were evaluated with paired t-test and binomial test (Daniel 1990). The effects of age, log(area), elevation, and isolation on species richness (S) were assessed using stepwise multiple regression: P(F-enter) < 0.10, P(F-remove) > 0.15. All statistical analyses were carried out in StatView 4.51 (Abacus Concepts 1996).

Results

The means of standardized species richness values in the five age categories are compared in Fig. 1. There is a significant increase of species richness between the first and second year of colonization followed by a significant decrease in species richness in years three to six. The oldest artificial islands (7 to 25 years) exhibit a small and non-significant increase in S/log(area). Natural ('climax') islands are even more species rich but the increase is still not significant. Identical results were obtained when residuals from either the regression of S on log(area) or the regression of log(S) on log(area)) instead of S/log(area) were used (not shown).

Changes in species richness on 34 re-sampled islands are summarized in Table 2. The initial increase in species richness is not significant – most likely a consequence of a low number of replicates (only four 1-yr old islands were re-sampled). Mean decrease in species richness on islands initially two to four years old is substantial (–6.6 species) but significant only in terms of paired t-test. Finally, there is, on the average, a very small (+1.7 species) but significant increase in S on islands 5 to 25 years old (Table 2).

Significant effects of age, log(area), elevation, and isolation over four age categories (data from re-sampling not included) are summarized in Table 3. Age, and area have a positive effect and distance a negative effect on S in the first two years. Area and elevation have a positive effect on S in the three to six years age category. In the last two categories (7 to 25 years and 'climax'), only area has a statistically significant effect on S.

Table 2. – Changes in species richness (S) on 34 re-sampled[*] islands. P_1 is significance of paired t-test, P_2 is significance of binomial test (increased vs. decreased).

Initial age (yrs)	Number of islands with S			Mean change (spp.)	P_1	P_2
	increased	decreased	no change			
1	3	1	0	+3.4	NS	NS
2 to 4	4	11	0	–6.6	0.003	NS
5 to 25	11	2	2	+1.7	0.048	0.022

[*] One year old islands were re-sampled after one year. Islands ≥ 2 years old were re-sampled after two years.

Table 3. – Results of stepwise regression analysis of species richness versus island age, log(area), elevation, and isolation (distance to the nearest shore).

Variable	Standardized partial regression coefficient	t	P
Years 1 and 2 (n = 21; adjusted R^2 = 0.854)			
Age	+0.376	3.49	0.002
log(area)	+0.799	8.36	< 0.001
Distance	–0.284	2.79	0.013
Years 3 to 6 (n = 23; adjusted R^2 = 0.728)			
log(area)	+0.643	5.32	< 0.001
Elevation	+0.306	2.57	0.015
Years 7 to 25 (n = 22; R^2 = 0.636)			
log(area)	+0.797	5.92	< 0.001
"Climax" (n = 5; R^2 = 0.817)			
log(area)	+0.904	3.66	0.033

Discussion

Changes in plant species richness during colonization/succession on studied islands (Fig. 1) can be easily interpreted in terms of Wilson's (1969) postulated sequence of 'equilibria'. The increase in species richness during the non-interactive stage and the decrease in interactive stage are both statistically significant. Decrease in species richness during the interactive stage is obviously due to the expansion of several strong clonal species (e.g., *Calamagrostis canescens, Phalaris arundinacea, Urtica dioica*). The increase in species richness in the assortative stage, however, is not significant. This generalization, based on 'space for time substitution' data, is confirmed by the observed development on re-sampled islands (Table 2). Moreover, the positive change in S during the assortative stage is significant based on both paired t- and binomial tests. As a whole, this is probably the first clear confirmation of Wilson's hypothesis for vascular plant communities on islands.

Statistical analysis of contributions of age, isolation, and elevation within individual age categories sheds some light on underlying processes (Table 3). Age affects S, positively and significantly, only on the youngest islands (change from the first to the second year). During this period, the negative effect of isolation is also significant. This means that only during this non-interactive period spatial isolation really matters. This restriction, of course, is scale-dependent. Maximum isolation in our system was only 250 m. Undoubtedly, for more isolated islands the effect of isolation would influence species richness over a longer time period. Kadon & Pulliam (1995) reported similar negative effects of isolation that were limited only to the initial stages of island colonization/succession.

Elevation is contributing positively and significantly to S only during the interactive stage (Table 3). This can be explained as increasing habitat separation of interacting species and, therefore, promotion of their coexistence. The positive effect of elevation declines on older islands. This is probably due to increasing representation of woody species (e.g., *Quercus robur, Rubus plicatus, Salix cinerea, Sorbus aucuparia*) that are less dependent on elevation within the available range (maximum = 2.5 m). In contrast to some studies on natural islands (e.g., Deshaye & Morisset 1988, Kohn & Walsh 1994), habitat diversity within the studied islands seemed to be relatively small and island area alone had therefore the dominant effect (Table 3).

Now, twenty years since our field work was accomplished, re-sampling of all the islands is highly desirable. This would substantially extend the time scale covered. Consequently, like in other studies of this kind (e.g., Rydin & Borgegård 1988, Roden 1998), new insights into the nature of the assortative phase of vegetation succession would be gained.

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Souhrn

Flóra cévnatych rostlin byla analyzována na 71 různě starých umělých ostrůvcích v 22 rybnících Třeboňské pánve (tab. 1). Časové změny druhového bohatství byly interpretovany ve světle Wilsonovy (1969) hypotézy vývoje biologických společenstev. V souladu s touto hypotézou byl pozorován statisticky průkazný vzrůst druhového bohatství v „neinteraktivní“ fázi (zde jeden až dva roky), následovaný průkazným poklesem v „interaktivní“ fázi (tři až šest let). Predikovaný vzrůst druhového bohatství v „roztřiďovací“ fázi (7 až více než 50 let) byl rovněž pozorován, ale statisticky průkazný nebyl (obr. 1). Tento sukcesní trend byl potvrzen vývojem flóry, který se udál na 34 opakovaně analyzovaných ostrůvcích. Na ostrůvcích reprezentujících roztřiďovací fázi byl vzrůst druhů průkazný (tab. 2, párový t-test, binomiální test). Vliv plochy ostrůvků, jejich stáří, převýšení a izolace (vzdálenost od nejbližšího břehu) na druhové bohatství během sukcesních fází byl rovněž analyzován. Pro ostrůvky staré 1–2 roky byl zjištěn statisticky průkazný pozitivní vliv plochy a stáří a negativní vliv izolace na druhové bohatství.

Pozitivní vliv plochy a převýšení byl průkazný pro ostrůvky 3–6 let staré. Pro starší ostrůvky byl průkazný pouze vliv plochy (tab. 3). Tato data pravděpodobně představují první potvrzení Wilsonovy hypotézy pro ostrovní společenstva cévnatých rostlin.

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