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Ecological network analysis in modeling of plant population dynamics

Grażyna Łaska, Aneta Sienkiewicz*

Department of Environmental Protection and Management, Białystok Technical University,
Wiejska 45a St, 15-351 Białystok, Poland;
*e-mail: a.sienkiewicz@pb.edu.pl

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Abstract. One of the most popular tools used in the process of modeling are ecological networks. Population dynamics of threatened plant species – *Pulsatilla patens* (L.) Mill. and commonly occurring taxon – *Carex digitata* L., was modeled using the package STELLA. The population of *P. patens* was studied in the years 2009-2011, at 16 sites, while the population of *C. digitata* was observed in the years 1987-2015, at the two sites in the natural and secondary oak-hornbeam forest *Tilio cordatae*-*Carpinetum betuli* Tracz. 1962 in the Supraśl Forest Division, Knyszyńska Forest. The input parameters for model construction were changes in the number of individuals and calculated on their basis birth and death rates. The proposed mathematical model of population dynamics implies that the probability of *P. patens* becoming a threatened species, evaluated on the basis of changes in the number of individuals is small, however it increases for *C. digitata* (in particular in the anthropogenically disturbed community). The results of simulations show that *P. patens* makes dynamically developing population characterized by an increase in the number of individuals with time in the period studied, disregarding the effect of natural and anthropogenic disturbances. In both *C. digitata* communities studied, a decrease in the number of individuals in the period studied is noted, and the rate of the decrease is much higher in the anthropogenically disturbed community, which means that the population is dynamically ageing.

Key words: population models, STELLA modeling, *Pulsatilla patens* (L.) Mill., *Carex digitata* L., probability of extinction, guidelines for protection.

1. Introduction

Over the past two decades, ecological models have become important tools for aiding decisions related to the conservation of biodiversity. Ecological models are frequently used to predict and assess the outcomes of conservation measures and ecosystem management strategies (Frank & Wissel, 2002; Leslie et al., 2003). Different ecological model types have been used, depending on the aim of modeling, e.g. species-distribution models to predict the future distribution of species (Attorre et al., 2013), individual species models to identify threatened plant species hotspots (Parviainen et al., 2009), model simulations to impact climate change on ecosystems (Fang et al. 2013) and models of population dynamics of endangered and threatened species (Beissinger & McCullough, 2002; Morris & Doak, 2002).

One of the most popular tools used in ecological modeling are networks. Networks are well suited for analysis of many types of ecological data (Raymond & Hosie, 2009). Complex structures of inter-related elements are pervasive in natural systems (Aloy & Russell, 2004; Green et al., 2005; Proulx et al., 2005) and network-based methods can provide an intuitive framework for understanding these systems. The importance of considering the overall ecosystem context when investigating elements of that ecosystem has long been recognized in the ecological sciences, but has been given recent re-emphasis (Jordán & Scheuring, 2004).

Network applications in ecology have received a recent surge of popularity (Green et al., 2005; Proulx et al., 2005). Networks offer insights into system-level properties that arise from the structure of the network, and which are not evident from the properties of the entities alone. Network-based methods can facilitate the analytical integration of an overall ecosystem with the dynamics of its individual elements (Jordán & Scheuring, 2004). Topology can provide information on the networks functioning and response to change (Jordán, 2001; Dambacher et al., 2003; Proulx et al., 2005). Moreover, the model could respond to the needed theoretical formalization of decision-making in ecosystem-based management (Rooney, 2001; Reynolds, 2005; Jensen et al., 2009).

Artificial neural networks (ANNs) are one of the easiest networks to understand, so they have been most commonly used in ecology. However, they are sensitive to composition of the training data set and to initial network parameters. Also, they are perceived as black box models (Özesmi et al., 2006). STELLA is a popular tool for dynamics modeling, which helps to put together conceptual diagrams and converts them into numerical computer models (Naimi & Voinov, 2012). It permits finding relationships that can be mathematical, logical, graphical or numerical (Costanza & Voinov, 2001). An increasingly popular method of modelling of uncertain and complex domains such as ecosystems and environmental management are Bayesian networks (BNs). They facilitate learning about causal relationships between variables based on probability distributions of the analyzed variables (Uusitalo, 2007). They offer the possibility of simulation and optimization of the levels of modeled factors, which gives background for making decisions supporting correct functioning of the natural environment (Łaska & Sienkiewicz, 2015).

The purpose of this study was to construct mathematical models of population dynamics of a threatened plant species – *Pulsatilla patens* (L.) Mill. and a common taxon – *Carex digitata* L., using the commercial available package STELLA. The specific objectives of this study were to: (1) develop dynamic models for estimating the probability of extinction of analyzed plant populations, (2) calibrate the models using available experimental data and (3) apply the models for assessment of the risk and development of guidelines for the protection of these populations.

2. Study area

The study of *P. patens* and *C. digitata* populations was conducted in north-eastern Poland, in the Supraśl Forest Division, Knyszyńska Forest. This is the forest area of approximately 17,439.94 ha located in the central part of the Forest (Forestry Commission Forest Management Plan Supraśl, 2006-2015) which belongs to the Natura 2000 network (Łaska, 2006, 2009). The population of *P. patens* was studied in the years 2009-2011, at 16 study sites (Łaska, 2010) and the population of *C. digitata* was studied in the years 1987-2015, at the two sites of natural and secondary oak-hornbeam forest *Tilio cordatae-Carpinetum betuli* Tracz. 1962 (Łaska, 2012).

3. Study species

Pulsatilla patens (L.) Mill. (Ranunculaceae) is a threatened plant species in Europe, listed in the Annex II of European Union Habitats Directive (92/43/ETY) (European Communities, 2004) and in Appendix I of the Bern Convention (Journal of Laws 1996, no. 58, item 263, 264). In Poland, *P. patens* has been a strictly protected species since 1958, it requires active protection (Journal of Laws, 2014, item 1409) and is classified to be protected within the program Natura 2000 (Journal of Laws, 2005, no. 94, item 795). In the "Red List of Vascular Plants in Poland" it is classified as critically endangered (E category) (Zarzycki & Szeląg, 2006) and in the "Red Data Book of Poland", it is listed as endangered (EN) species (Kaźmierczakowa et al., 2014).

Carex digitata L. (Cyperaceae) is a commonly occurring in the temperate zone of Europe and Asia, mesotrophic oak-hornbeam species, growing most often in the shady deciduous forests (Matuszkiewicz, 2001; Zarzycki et al., 2002), it also occurs in other habitats of diversified natural communities (in mixed deciduous and coniferous forests). *C. digitata* also appears in the anthropogenically disturbed communities (on the clear-cuts, in pine cultivations, in the secondary forest communities with an artificial pine stand) (Łaska, 2006, 2012).

3. Methods

3.1. Population dynamic model built with STELLA

Mathematical models of population dynamics of *P. patens* and *C. digitata* were built using the stock and flow model software (STELLA II 3.0.7) with an icon based interface and availability of array functions (Costanza & Voinov, 2001; High Performance Systems Inc., 2002). After Doerr (1996) it is assumed that the system dynamics is a concept that considers the dynamic interaction between the elements of the studied system and can help to understand their behavior over time, build models, identify how information feedback governs the behavior of the system and develop a strategy for better management of the studied system.

The initial parameters for construction of the population dynamics model were the changes in the number of individual plants of *P. patens* and *C. digitata*, counted in defined time intervals. In the mathematical model it was assumed that a population grows exponentially according to the birth rate and dies according to the death rate. It was also assumed that the size of a population determined by the birth and death rates (Falińska, 2012) does not depend on the natural (biotic and abiotic) and anthropogenic disturbances. The estimation of the probability of population extinction over the next 10 years is made assuming that birth rate is constant, while the death rate depends on the nominal death rate assumed in the model, normal distribution with a mean of nominal death rate and statistical parameters assumed as its arguments (mean and standard deviation) (Hannon & Ruth, 1997). Also the mean size of population was taken into account, defined as the ratio of the total number of individuals in a certain time interval to that in the assumed period of counting. The dynamic simulation model was developed using a time step of 0.25 years and the Euler`s integration method.

4. Results

4.1. Dynamics of population *Pulsatilla patens* and *Carex digitata*

On the basis of the counted numbers of *P. patens* individuals, the size of its population was found to increase from 165 in 2009 to 267 in 2011. At nine sites the number of individuals was observed to increase, at 5 it decreased, while at 2 it remained the same. The highest number of *P. patens* individuals in 2009 was at site 1 at which 82 plants were noted, while in 2011 at the same site the number of individuals grew by 89%. In 2011 only at two sites, number 8 and 13, no plants of this species were noted, (Fig. 1) (Łaska & Sienkiewicz, unpubl. data). On the basis of this data the calculated birth rate for *P. patens* population is 26%, while the death rate is 7%.

The number of *C. digitata* individuals changed slightly in the population from the natural oak-hornbeam community and declined in the population from the anthropogenically disturbed community. At the beginning of the observation period (1987), a greater number of *C. digitata* individuals in the population was observed at the anthropogenically disturbed site (378 individuals) than in the natural oak-hornbeam community (63 individuals) (Łaska, 2012). After 29 years (2015), in the natural oak-hornbeam community, the number of individuals remained relatively stable (from 63 to 55 individuals) and at the anthropogenically disturbed site it declined (from 378 to 96 individuals) (Łaska, unpubl. data). The calculated birth rate for *C. digitata* population from the natural oak-hornbeam community was 1.5% at the death rate 2.1%, while for the population from the anthropogenically disturbed community it was 0.5% at the death rate 3%.

4.2. Model of population dynamics *Pulsatilla patens* and *Carex digitata*

The structure of the model describing the population dynamics of *P. patens* and *C. digitata* is shown in Figure 2. The model consists of two stocks (rectangles): Population and Sum population and eight converters (circles): Births, Deaths, Death rate, Nominal death rate, Death rate distribution, Death rate distribution control, Current population, Average population size. The model contains three flows and ten storage connections needed for the network analysis. Parameters of this model are determined by the func-

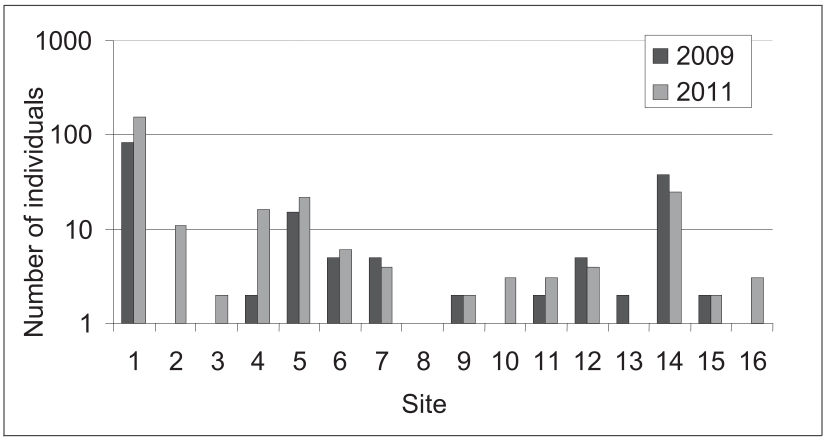
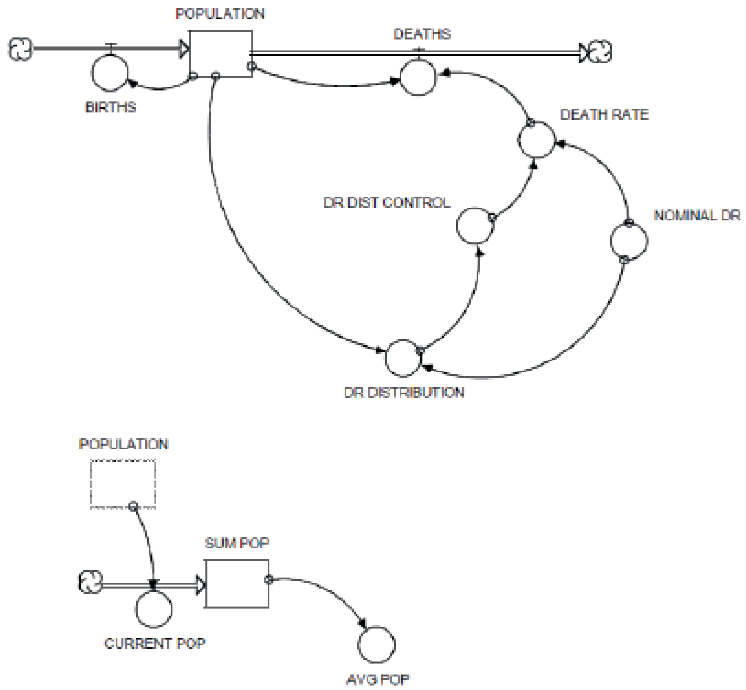


Figure 1. Dynamics of the *Pulsatilla patens* (L.) Mill. population in the Supraśl Forest Division, Knyszyńska Forest (Łaska & Sienkiewicz, unpubl. data)

tions defined in Figure 2. Their analysis permitted evaluation of the probability of extinction of the analyzed plant populations.

On the basis of the simulation performed for the assumed birth and death rates, the size of *P. patens* population was found to increase over the period of 10 years for which the calculation was made (Fig. 3). The population size increased by 24%, at the mean number of individuals for the period of 10 years of 273 and the nominal death rate of – 0.18 (Table 1). As follows from the results, up to the fourth year of the simulation the rate of population increase is relatively constant, in the longer time period events of periodical decrease in the number of individuals are noted, in particular in the fifth and eighth years of simulation.

According to the simulation results for *P. patens* population, at the low death rate with respect to the birth rate, the probability of the population becoming endangered because of the decrease in population size is very small. The periodical decrease in the number of individuals does not exceed the population size assumed as input datum in the

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POPULATION(t) = POPULATION(t - dt) + (BIRTHS - DEATHS) * dt
INIT POPULATION = 267
 INFLOWS:
    BIRTHS = 0.26*POPULATION
 OUTFLOWS:
    DEATHS = DEATH_RATE*POPULATION
SUM_POP(t) = SUM_POP(t - dt) + (CURRENT_POP) * dt
INIT SUM_POP = 0
 INFLOWS:
    CURRENT_POP = IF TIME>0 THEN POPULATION ELSE 0
AVG_POP = IF TIME>0 THEN SUM_POP/(TIME-0) ELSE 0
DEATH_RATE = (IF DR_DIST_CONTROL>NOMINAL_DR THEN DR_DIST_CONTROL ELSE
NOMINAL_DR)*1+0*DR_DIST_CONTROL+0*NOMINAL_DR
DR_DISTRIBUTION = NORMAL (NOMINAL_DR,0.005*POPULATION)
DR_DIST_CONTROL = IF (DR_DISTRIBUTION>=0.01) AND (DR_DISTRIBUTION<=1) THEN
DR_DISTRIBUTION ELSE 0.01
NOMINAL_DR = (EXP(- .01*TIME)* .19+ .01)*1+ .07*0
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Figure 2. The structure of mathematical model of population dynamics of *Pulsatilla patens* (L.) Mill. and *Carex digitata* L. and the functions describing the model parameters

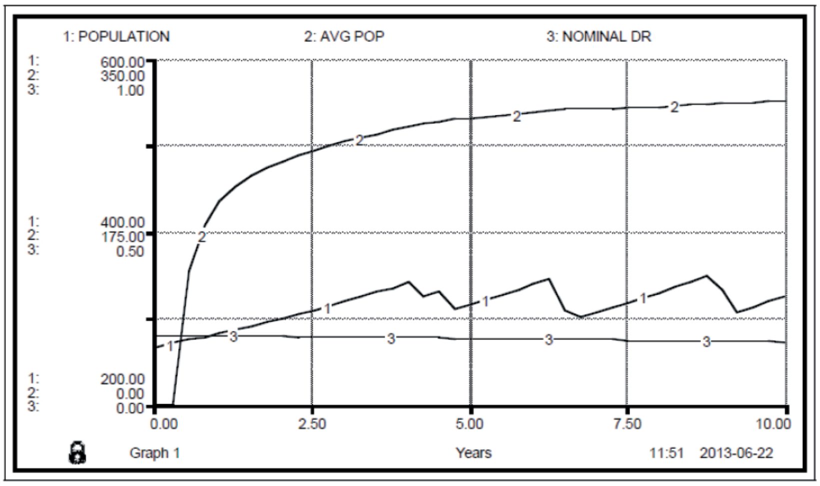

Figure 3. Simulation of the population of *Pulsatilla patens* (L.) Mill. population size dynamics, mean population size and nominal death rate for the 10 year period of calculations

Years	POPULATION	AVG POP	NOMINAL DR
0	267.00	0.00	0.20
1	283.02	0.00	0.20
2	300.54	141.51	0.20
3	319.70	194.52	0.19
4	340.68	225.81	0.19
5	277.68	248.79	0.19
6	296.92	253.60	0.19
7	318.02	259.79	0.19
8	287.19	267.07	0.19
9	308.62	269.30	0.18
Final	332.18	273.24	0.18

Table 1. *Pulsatilla patens* (L.) Mill. population size, mean population size and nominal death rate in particular years of the 10 year simulation period

model. It means that disregarding the effects of natural and anthropogenic disturbances, the population of *P. patens* is dynamically developing with the number of individuals increasing with time.

The simulation of population dynamics for *C. digitata* from the natural oak-hornbeam site and the anthropogenically disturbed site, performed for the assumed birth and death rates for the 10 year period, proved a decrease in the population size (Figs 4a, b). In the natural oak-hornbeam community the decrease in number of this species individuals decreased by 20%, at the mean population size of 44 individuals and the nominal death rate of – 0.02 (Table 2a). At the anthropogenically disturbed site, the decrease reached 82%, at the mean population size of 24 individuals and the nominal death rate of – 0.03 (Table 2b). The rate of *C. digitata* population size decrease was much greater in the anthropogenically disturbed community than at the natural oak-hornbeam site.

According to the results of simulation for *C. digitata* population, at the high death rate with respect to the birth rate, the probability of the population becoming endangered increases. It is particularly pronounced for the population from the anthropogenically disturbed community, in which the greatest changes in population size (from 378 to 96 individuals) were noted at the lowest birth rate (0.05%). For *C. digitata*, at both study sites a decrease

a) b)

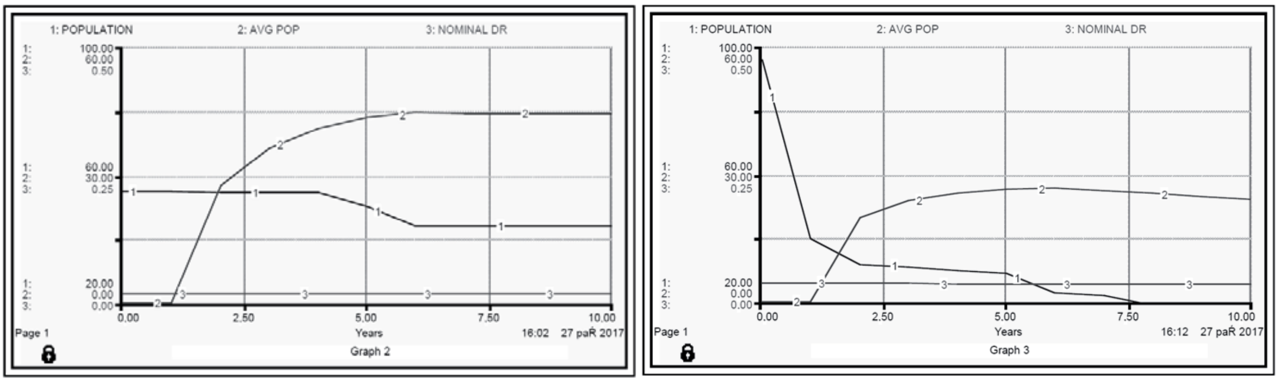

Figure 4. Simulation of *Carex digitata* L., population size, mean population size and nominal death rate for the 10 year period of calculations, for a) the natural oak-hornbeam community, b) the anthropogenically disturbed community

in the number of individuals was observed in the 10 year period of study, which indicates that it makes a dynamically ageing population.

5. Discussion

Ecological network analysis is an important tool to understand the whole-system interactions. The edges in the network show direct relationships between entities, and so the network explicitly depicts the local structure within the data, allowing the topology of the system as a whole to emerge from the individual relationships.

The explicit characterization of relationships by edges in a network has potential advantages for the visual representation of complex data, but perhaps more interestingly, allows subsequent exploration and analyses to focus on the relationships themselves (Raymond & Hosie, 2009). Moreover, networks can be used to integrate ecological data with other types of data such as economic (Janssen et al., 2006), not merely in visual syntheses but in analytical integrations that allow the effects of human impacts on ecosystems to be explored (Dambacher et al., 2003; Fath, 2004; Rooney et al., 2006; Dambacher & Ramos-Jiliberto, 2007).

However, Lek (2007) has reported that being simplified representations of the reality, the simulated ecological models can never be the same as the real nature, i.e. their results are somewhat uncertain. The uncertainty of an ecological model is caused by both the lack of knowledge (i.e. data imperfection) and the variability of models and parameters (models' sensitivity). Data may contain errors that result from either sampling, measurement or estimation mistakes (Regan et al., 2002). Uncertainty analysis in the ecological models implies the identification of errors, inexactness, imperfection and unreality in the models (Li & Wu, 2006; Wu et al., 2006). The considerations of uncertainty in the

Table 2. *Carex digitata* L., population size, mean population size and nominal death rate in particular years in particular years of the 10 year simulation period in a) the natural oak-hornbeam community, b) the anthropogenically disturbed community

a)

Years	POPULATION	AVG POP	NOMINAL DR
0	55,00	0,00	0,02
1	54,95	0,00	0,02
2	54,50	27,47	0,02
3	54,45	36,48	0,02
4	54,41	40,97	0,02
5	50,06	43,66	0,02
6	43,90	44,73	0,02
7	43,88	44,61	0,02
8	43,85	44,52	0,02
9	43,83	44,44	0,02
Final	43,80	44,38	0,02

b)

Years	POPULATION	AVG POP	NOMINAL DR
0	96,00	0,00	0,04
1	39,58	0,00	0,03
2	31,53	19,79	0,03
3	30,60	23,70	0,03
4	29,71	25,43	0,03
5	28,84	26,28	0,03
6	22,57	26,71	0,03
7	21,93	26,12	0,03
8	18,50	25,59	0,03
9	17,98	24,81	0,03
Final	17,48	24,12	0,03

ecological models have lately increased for ecological research areas, such as risk assessment of species (Regan et al., 2003) or biological conservation (Wintle et al., 2003).

In spite of this, models of population dynamics are employed as useful tools for assessment of a population's risk of extinction or potential for growth. The use of these models to predict the risk of plant populations is very important in developing effective strategies for conservation of particular plant species. With sensitivity, elasticity, and perturbation analyses, users can assess the impact of changes in demographic rates on a population's growth or decline (Mills & Lindberg, 2002). Through such analyses the model can be used to assess the impact of management actions, to indicate which variables are most critical for prioritized data collection, and ultimately to guide allocation of conservation resources. There are many examples of models that could contribute to the environmental management practices (Neto et al., 2006; Ouyang et al., 2007; Ouyang, 2008; Kumar et al., 2008; Garedew et al., 2009; Qaiser et al., 2012; Sandker et al., 2012). However, Marrero-Gómez et al. (2007) suggest that models of population dynamics must be used with caution, especially when the results are to be used for decisions on practical species conservation and management.

The tested models, using STELLA, were built on the basis of relationships between analyzed variables. The outcome of a simulation is entirely dependent on these relationships and the input data. Therefore, any output always needs to be analyzed in relation to the input assumptions (Garedew et al., 2012). Stella is well suited for ecological applications, among other reasons because of the clear visualization of the population structure. The software is also valued for the clarity of the density dependent feedback that controls the eventual size of the plant populations. We found the system's dynamics approach useful in modeling the population dynamics of threatened plant species – *P. patens* and commonly occurring taxon – *C. digitata*. The results of the model for *P. patens* proved that it makes a dynamically developing population with the number of individuals growing with time, on disregarding the effects of natural and anthropogenic disturbances. The population of *C. digitata* was found to be dynamically ageing as in both communities studied the number of individuals decreased in the time period considered. The results obtained for *C. digitata* were the response to changes taking place in the two plant communities studied. In the natural oak-hornbeam community, the results of ecological observations over the period of 1987-2015 reveal fluctuations in the number of individuals, leading to a relative dynamic equilibrium of *C. digitata* population, ensuring the stability of the phytocenosis. The fluctuations take place at a low number of individuals (65-55) (Łaska, in press) at a low value of death rate. The low birth rate in the *C. digitata* population in the natural oak-hornbeam forest habitat is a result of strong interspecies competition in the rich herbal layer.

The changes in the dynamics of vegetation observed over the period of 1987-2003 in the anthropogenically disturbed community (pinetization) are different. The disturbance was the removal of pine and spruce trees from the tree stand. As a result of positive selection, the deciduous species (*Carpinus betulus*, *Corylus avellana*) are preferred in the community. The dynamic changes taking place in the forest secondary community observed in 1987 indicated the process of degeneration, while at present the observations imply the process of regeneration, which includes the renewal of the structure and functioning of the community developing towards its natural form. In response to the dynamic development of vegetation in this community the size of *C. digitata* population undergoes rapid changes at a high number of individuals and finally the number of individuals decreased from 378 to 96 plants, which is described by a high death rate.

However, the simulation of *P. patens* population dynamics was performed for a relatively short time (3 years) which is insufficient to answer a wide range of questions about its further fate. The conclusions drawn for *C. digitata* population are more reliable as the model of its population dynamics was constructed on the basis of long-term studies (29 years). The models should be tested using subsequent field data and several scenarios assuming different changes in the number of individuals in populations. Moreover, the model testing would permit verification of the parameters which would ensure correct population functioning. We are currently thinking about expanding the constructed model by adding biotic and abiotic factors affecting the population dynamics, especially the influence of climate change on seasonal variations in the number of *P. patens* individuals, since according to Wójtowicz (2004) a potential threat for this species is climate warming and high instability of thermal conditions in the winter. Similarly in the case of population viability of the narrowly endemic *Helianthemum juliae* Marrero-Gómez et al. (2007) assumed that herbivores are not a significant factor, because they did not observe any damage that could be attributed to herbivores and all observed deaths in the field were caused by summer drought or natural senescence. One of the most important aspects in these models is the duration of demographic monitoring that is needed to adequately estimate environmental variability.

6. Conclusions

Presented models are useful tools in modeling the population dynamics of threatened plant species – P. patens and commonly occurring taxon – C. digitata. The models should be tested using subsequent field data and several scenarios assuming different changes in the number of individuals in populations.

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