

Does the Mean Individual Biomass (MIB) of carabids as a bioindicator of forest succession follow a logistic function? – Examples from Western German beech and Polish Scots pine forests

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Successional processes are a common element of commercial forest monocultures. Here, after harvesting and replanting the trees, large parts of the forest ecosystem start from early successional stages at the same time. Of course, succession depends on various site-dependent factors, but there are patterns broadly relevant for successional processes in forestry. One of these patterns may be underlying the course of development of epigeic ground-beetle assemblages (Coleoptera: Carabidae) as can be followed, e.g., by monitoring the Mean Individual Biomass (MIB) of carabids over time. In Western German beech stands of increasing age (14 stands, 1 – 165 years) and in Polish Scots pine forests (14 stands, 21 – 119 years) MIB has been described by a logistic growth function showing different shapes probably as a consequence of good vs. poor soil quality. A mathematical model has been developed which regresses field data on ecological succession and supplies information on, e.g., the initial degradation, the onset and speed of succession, and the ecological capacity of the geographical region and forest type. The model is subject to further amendment.

Key words: Carabidae, mean individual biomass, MIB, logistic function, bioindicator, forest, succession

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INTRODUCTION

Nowadays, commercial forests are common in most European countries such as Germany and Poland. Although the geographical and climatic prerequisites may be different, commercial forestry similarly comprises tree monocultures at a uniform age. Therefore, after harvesting and replanting the trees, large areas of the forest eco-

system undergo a uniform successional process (secondary succession). In the run of succession the species composition changes as one of the functions of forest productivity (e.g. Neumann 1971, Szyszko 1990, Skłodowski 2006, Skłodowski 2009).

Carabid beetles (Coleoptera: Carabidae) react to changes in environmental conditions by changes

in the species inventory, abundances, and activity patterns. Therefore, they are useful bioindicators in succession research (Szyszko 1990, Halme & Niemelä 1993, Rainio & Niemelä 2003, Koivula 2011). Their composition has been extensively studied in Scots pine or spruce monocultures in the northern hemisphere (Szyszko 1990, Koivula & Niemelä 2002, Phillips et al. 2006, Pohl et al. 2007, Schwerk 2008) as well as in Western German beech and Douglas fir forests (Schreiner 2011, Schreiner et al. 2011, Schreiner & Schwerk 2011). Frequently, the mean individual biomass of carabids (MIB) has been used as a major tool of comparison between different stages of forest succession. As a general rule, MIB increases over the run of succession (Szyszko 1990, Serrano & Gallego 2004, Cárdenas & Hidalgo 2007, Schwerk & Szyszko 2007, Schwerk 2008, Schwerk & Szyszko 2009, Schreiner 2011, Šerić Jelaska et al. 2011).

While successional processes on the one hand depend on various site-dependent factors there are, on the other hand, certain patterns that have general relevance in forest succession as in many other biological systems. One of these patterns (i.e. logistic growth; Turchin 2003) may be underlying the course of development of epigaeic ground-beetle assemblages. Schwerk (2008) introduced a model of succession using a logistic equation for describing the growth of populations. In order to further study this model and to utilize it for field-data regression we determined the MIB of carabids over time in two forest areas quite different in nature:

- a) Western German beech forests on “rich” loam soil (Schreiner 2011), and
- b) Polish Scots pine forests on “poor” sandy soil (Schwerk 2008).

Generalized logistic functions base on a differential equation as given below in Eq. 1 (Draper & Smith 1998, Britton 2005).

$$f'(t) = k \cdot f(t) \cdot (G - f(t)) \quad (\text{Eq. 1})$$

In this term, G represents the study area’s capacity, which might be ecologically interpreted as the maximum MIB that can be reached – theoretically – in a given forest. The term’s k is a constant comprising all other parameters influencing succession. Solving this differential equation leads to the function given below (Eq. 2).

$$f(t) = G \cdot \frac{1}{1 + e^{-k \cdot G \cdot t} \left(\frac{G}{f(0)} - 1 \right)} \quad (\text{Eq. 2})$$

On the basis of Eq. 2 MIB data from German and Polish forests have been regressed with the aim of inferring certain characteristics of the run of secondary succession in our study areas, e.g. the initial degradation of the study sites, the onset and speed of succession, and the ecological capacity of the sites (or the greater geographical region and forest type, respectively).

MATERIALS AND METHODS

Carabids were collected by pitfall traps (Barber 1931) on 14 Western German beech stands of increasing age (1 – 165 years) as well as on 14 Polish stands afforested with Scots pine (21 – 119 years). The German sites were followed over the complete vegetation period of 2009 with 3 traps per stand (Schreiner 2011), while the Polish sites were harvested in 3 consecutive years (2004 – 2006) by using only 1 trap per stand (Schwerk 2008). Hence, both areas were comparable with regard to the overall number of trap-years. In addition, both study areas had a similar history of forestry.

When 3 traps per stand were placed, each of them was set 5 – 10 m apart. Boundary effects were avoided by placing all traps at least 20 m away from the site’s edges (den Boer 1977).

The beetles were counted and stored in commercial EtOH 70 % v/v before determination to the species. The individual biomass was obtained by using values from Szyszko (1990) or applying the mathematical term according to Szyszko

(1983) to well-known beetle-length data (Müller-Motzfeld 2004).

MIB development over time (i.e. MIB values of study sites of increasing age) was regressed according to the logistic function indicated above. MIB regression functions were drawn up by using the Microsoft Excel solver programme.

The total carabid catching results in German beech and Polish pine forests are given in Table 1. More than 10 times as many carabids were collected on “rich” German loam soil as compared to “poor” Polish sandy soil. In addition, more than 60% of the carabids caught in German beech forests belonged to the genus *Carabus* while the corresponding figure in Polish pine forests was just over 30%.

RESULTS

As shown in Figure 1 for Western German beech forests, MIB values of the individual study sites

Table 1. Overall stand characteristics and carabid catching results in German beech and Polish Scots pine forests.

Stands	Country	Soil quality	No. of stands	Year(s) of observation	Traps/stand	No. of carabids	Thereof No. of <i>Carabus spec.</i> (dominance)
Beech	Germany	Loam (“rich”)	14	2009	3	5,536	3,356 (60.6 %)
Scots pine	Poland	Sand (“poor”)	14	2004 – 2006	1	493	160 (32.5 %)

Table 2. Mean individual biomass (MIB) values of all study sites and years (complete vegetation periods)

a) Beech, Germany
(3 traps per site)

Area	Age 2009 (years)	MIB 2009 (mg)
B1	1	156.9
B2	1	512.4
B3	3	265.2
B4	4	402.4
B5	13	428.3
B6	20	317.9
B7	26	697.4
B8	28	666.7
B9	52	708.5
B10	78	622.1
B11	146	654.3
B12	146	700.2
B13	152	426.2
B14	165	733.6

b) Scots pine, Poland
(1 trap per site and year)

Area	Age 2004 (years)	MIB 2004 (mg)	MIB 2005 (mg)	MIB 2006 (mg)
SP1	21	243.1	230.3	435.6
SP2	25	349.3	185.8	208.0
SP3	35	152.3	362.4	306.3
SP4	36	255.5	489.1	468.8
SP5	40	60.1	235.1	256.7
SP6	40	138.0	354.0	175.5
SP7	44	399.3	314.2	314.2
SP8	47	106.4	56.1	432.0
SP9	51	288.0	390.8	450.4
SP10	61	347.7	216.4	-*
SP11	62	280.5	400.5	700.8
SP12	117	126.0	-*	750.0
SP13	117	189.4	433.3	471.2
SP14	117	485.0	-*	680.0

* Trap damage by game

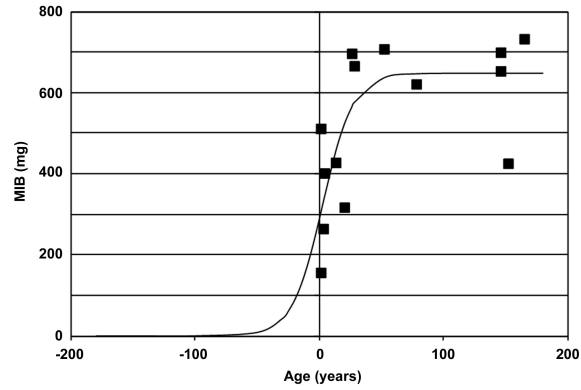


Fig. 1. Logistic regression curve – Relationship between age of the Western German beech stands (years) and mean individual biomass of carabids (mg)

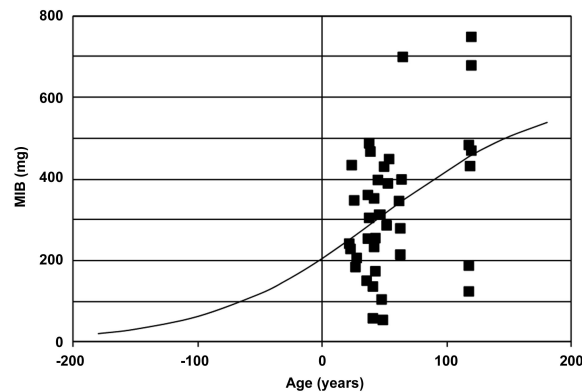


Fig. 2. Logistic regression curve – Relationship between age of the Polish Scots pine stands (years) and mean individual biomass of carabids (mg)

(Table 2a) can be regressed by a logistic function with $G = 648.690$ mg and $k = 1.264 \times 10^{-4}$. Hence, a steep gradient can be seen that starts from a rather high baseline MIB at $t = 0$ (secondary succession: incomplete degradation of the stands). Moreover, the inflexion point of the curve is already reached a few years after the present beech trees were planted, i.e. an early onset of succession (or a short “time to maximum speed”, Table 3). The steep slope of the curve (high “speed of succession”) reaches a plateau value at about 650 mg (climax MIB) in old stands (Table 3).

The logistic MIB function resulting from Polish pine forests is depicted in Figure 2. Its characteristics are $G = 611.680$ mg and $k = 2.429 \times 10^{-5}$. Although starting from a high baseline MIB (Table 2b) comparable to the situation of beech stands (again incomplete degradation in the scope of secondary succession), the curve’s gradient is much lower and corresponds to a long time to maximum succession speed (Table 3). MIB values already peak at about 610 mg in old stands (Table 3).

Table 3. Succession characteristics inferred from logistic MIB functions in German beech and Polish Scots pine forests

Function characteristic	Corresponding ecological parameter	German beech stands (MIB)	Polish Scots pine stands (MIB)
Intersection with Y axis (MIB axis)	Initial degradation level	291.6 mg	205.8 mg
Gradient at inflexion point	Maximum speed of succession	13.3 mg/year	2.3 mg/year
X value (t value) at inflexion point	Time to maximum speed (may include an initial delay)	2.5 years	45.3 years
Function's G value	Climax capacity of forest	648.7 mg	611.7 mg

DISCUSSION

A main result of this study is that rather different field data on MIB distribution over time can be regressed by using the same logistic function. In this respect, although it is difficult to pinpoint a definite regression coefficient for logistic functions, MIB values from Polish Scots pine seem to deviate further from the curve than those from German beech. In both types of forests, however, the results of logistic regression can be transferred into ecological characteristics of succession that are very reasonable. Both the high number of carabid individuals and the huge proportion of large ones (genus *Carabus*) caught in Western German beech forests vs. Polish Scots pine stands, match the earlier onset and steeper course of the succession curve in Western Germany. Figures like these may be expected when comparing a "rich" ecosystem (on loam soil) to a "poor" one (on sandy soil), as the number and species composition of carabids is directly influenced by the ground-ecological factors effective during larval development. However, other characteristics may also influence the pattern of egigaic predators. E.g., similar to our study, a high baseline MIB was observed in particularly humid Polish habitats (Kwiatkowski 2011). This result was explained not only by soil richness but also by the size of clear cuts and type of soil preparation. An influence of the type of soil prepa-

ration on the formation of carabid coenoses was also shown by Skłodowski (2005).

Generally, we did not follow succession in a single forest stand through the years but monitored German and Polish stands of variable age over a rather short observation period of 1 and 3 years, respectively. This may have led to differences in certain (e.g. geological) prerequisites between the individual sites, although we tried to maximize site comparability by checking beforehand on the beetle-size development (which was modestly increasing in ageing forests) and other site characteristics such as byplants and stand history (Schreiner et al. 2011, Schwerk 2008). In terms of the catching methodology and number of trap-years compared, our data are in line with current research standards in carabidology (Kotze et al. 2011). Both the "time effort" and "trap effort" as defined by Lövei and Magura (2011) are comparable between the German and Polish sites since the same number of traps was used over a similar period of time (i.e. a complete vegetation period). In theory, it is well possible that succession, like many other biological systems (Turchin 2003), follows a logistic growth function. The sigmoid shape of logistic curves not only reflects a constant increase of MIB during succession, which was described by a host of previous data (Szyszko 1990, Serrano & Gallego 2004, Cárdenas & Hidalgo 2007, Schwerk & Szyszko 2007,

Schwerk 2008, Schwerk & Szyszko 2009, Schreiner 2011, Šerić Jelaska et al. 2011), but also matches the prior MIB-based model of succession (cf. Schwerk 2008, Schwerk & Szyszko 2011). The first model amends the logistic function by an “initial delay”, which may be reasonable in some sites (e.g. with primary succession on post-industrial areas) but is rather difficult to calculate. The “time to maximum speed” of succession, as defined in the present work by the t value at the curve’s inflexion point (Table 3), comprises the “initial delay” of the former model and equals the succession speed between times of (almost) no succession and times of faster succession. Therefore, in the case of delayed succession, the logistic model, as proposed here, may be slightly inaccurate. Also, our model curve describes primary succession courses starting at $MIB = 0$. Thus, in the case of secondary succession (initial $MIB > 0$) the curve begins at negative t values. We can assume that the real situation differs from what our curve suggests for the early years of succession (after the curve intersects with the Y axis) due to effects overlapping from the site’s prior use. Although this error may be small, it should be the object of further research along with the generation of a greater field-data base for logistic functions of succession (more sites or prolonged observation time). Increasing data will allow to generate better curves for various geographical regions or areas with forest monocultures, to which local catching results can be compared in order to detect areas of ecological imbalance (e.g. “hot spots” prone to pest attacks). In this context, a method has been developed to predict pest epidemics by relating MIB to the age of the habitat in Polish commercial forests (Szyszko 1990).

CONCLUSION

A mathematical model has been developed based on logistic growth, which regresses MIB-based field data on succession and supplies information on ecologically relevant aspects such as the initial degradation, the onset and speed of

succession, and the ecological capacity of the geographical region and forest type, especially when looking at forest monocultures. This may help to identify areas where succession is disturbed. More data are needed to improve our model.

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