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Glacier foreland colonisation: distinguishing between short-term and long-term effects of climate change

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Abstract By comparing short-term (6 years) observations with long-term (>100 years) community changes reconstructed from the chronosequence along a glacier foreland, I show that the colonisation of recently deglaciated terrain by invertebrates may constitute a process reacting sensitively to temperature fluctuations. Early colonising stages (<30 years old) currently develop faster, and intermediate successional stages (30–50 years old) slower, than would be indicated by the long-term chronosequence pattern. These differences between the chronosequence approach and direct observation can be explained by a simple model relating the rate of community evolution to the temperature record. It would mean that an increase of 0.6°C in summer temperatures approximately doubled the speed of initial colonisation, whereas later successional stages were less sensitive to climate change. The present situation appears to result from unusually warm summers around 1950 and a warm period accelerating glacier retreat since 1980. In contrast to the long-term trend, all except the youngest communities have suffered a loss in diversity in recent years.

Keywords Alpine environment · Arthropods · Epigean fauna · Global warming · Primary succession

Introduction

Cold habitats at high altitudes and high latitudes where organisms have to thrive under unfavourable environmental conditions are considered particularly sensitive to climate fluctuations (Walker 1995). Even if evidence for this sensitivity is ambiguous, several ecological key processes in high-alpine ecosystems turn out to be strongly affected by temperature, in many cases by indirect effects. Temperature appears to be a key factor controlling acid-base balance in alpine lakes through production and decomposition (Psenner and Schmidt 1992), accumulation of heavy metals in fish in response to altered metabolic rates (Köck et al. 1996), and nitrogen and carbon turnover of soils by effects of snow cover duration (Williams et al. 1998). Warming may force plant species to migrate upwards (Grabherr et al. 1994) and it may cause shifts in dominance of plant guilds (Harte and Shaw 1995).

Colonisation and establishment of viable populations is a fundamental ecological process which most existing ecosystems have gone through at some time in the past and which has not yet been studied in relation to temperature changes in high-alpine environments. Barren moraines uncovered by receding glaciers represent a natural experiment and offer an almost ideal opportunity for studying colonisation and the ensuing primary succession. World-wide glacial retreat over the last 150–200 years created spatially ordered chronosequences of moraines of increasing age. It is well recognised, however, that the chronosequence approach can represent the historical development correctly only if environmental conditions remain constant (Matthews 1992). Thus, although invaluable for the purpose of reconstruction, these long-term sequences need to be verified by direct observation. In fact, in some glacier forelands it was shown that incorrect predictions about future development can result from local disturbance or from differing distances of coloniser pools (Matthews and Whittaker 1987; Fastie 1995). Since glacial recession is a consequence of climate change, constant conditions cannot be assumed. Therefore, the objective here was to compare directly observed short-term (5–6 years) community changes with the long-term changes (>100 years) inferred from the chronosequence. Yearly records of surface-active invertebrates were used for this purpose.

The basis was a previous chronosequence study of the Rotmoos glacier foreland in the Austrian Central Alps (Kaufmann 2001; Kaufmann and Raffl in press). It was shown that invertebrate communities were predominantly determined by successional site age, with additional local influences of moisture and sun exposure. Commu-

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nities evolved rapidly over the first 50 years with high species turnover, but at later stages the invertebrate communities almost stagnated and successional progress of vegetation slowed. Within 150 years the fauna attained a state similar to old adjacent sites, whereas vegetation did not. These results were largely consistent with the abundant information on plant succession from other glacier forelands (reviewed by Matthews 1992). The continuous record of invertebrates from 1995–2000 yielded a snapshot of short-term changes for comparison with the chronosequence trends. Such comparisons are rare for vegetation (e.g. Whittaker 1991), and, to my knowledge, are new for invertebrate fauna.

Materials and methods

Study area and sampling

Rotmoos glacier foreland is located in the Austrian Central Alps well above the treeline (46°50′N, 11°03′E, elevation 2,300–2,450 m), the chronosequence representing 140 years stretching over a length of 2 km. The terminal moraine delimiting the glacier foreland is dated 1858, while a second prominent moraine ridge is the remnant of a short glacier advance around 1920. A detailed site description was given by Kaufmann (2001).

Surface-active invertebrates were sampled by pitfall traps from 1995 to 2000. Sampling was done over the entire growing season from 1995 to 1999; in 2000 the sampling schedule was reduced to three sampling periods. A reduced set of traps was in operation in 1995. Seventy traps were spread along the area (map given in Kaufmann 2001), 48 of which belonged to the chronosequence proper. Eleven additional sites in front of the terminal moraine, ice-free for nearly 10,000 years, served as a reference. Eleven sites within the glacier foreland which frequently experience flooding behaved differently and were excluded from the current analysis.

The dominating invertebrate groups, beetles, spiders, and harvestmen, were determined to species level in all years; other invertebrate groups were included at higher taxonomic levels. The trapped and identified material amounted to 86,000 individuals belonging to 170 taxa.

Yearly records of glacial retreat have existed since 1892. Reports and photographs give additional information about past glacier snout positions; thus average retreat rates could also be estimated for the period from 1858 to 1892. These data were compiled by Juen (1998) and facilitated estimation of the dates of deglaciation for all sampling sites with an accuracy of ±2 years back to around 1890. Estimates for older sites are less accurate.

A climate record with monthly temperatures going back to 1851 is available from Vent, a small village located in a neighbouring valley 8 km to the east at an altitude of 1,900 m (by courtesy of Department of Meteorology and Geophysics, University of Innsbruck). Here I use summer temperature averages from June to September which represent the growing season at the investigation site. According to recordings since 1995, temperatures in the Rotmoos glacier foreland are 3.4°C lower than in Vent.

Analyses and statistics

Yearly catches at all sites were ordinated by Detrended Correspondence Analysis (programme CANOCO 4.0, ter Braak and Smilauer 1998). Rare species (<100 individuals total catch) were excluded from ordination analysis, but this had no effect on the results. A total of 57 taxa comprising 84,000 individuals remained in the analysis. All taxa were included for assessing diversity.

The first ordination axis was clearly identified as the time axis showing the successional progress of the community. Scaling options were chosen such that changes in ordination scores indicated species turnover. With this approach, following Whittaker (1991), between-site changes of ordination scores represent the chronosequence pattern while within-site changes over the years yield the directly observed short-term trends in ordination space.

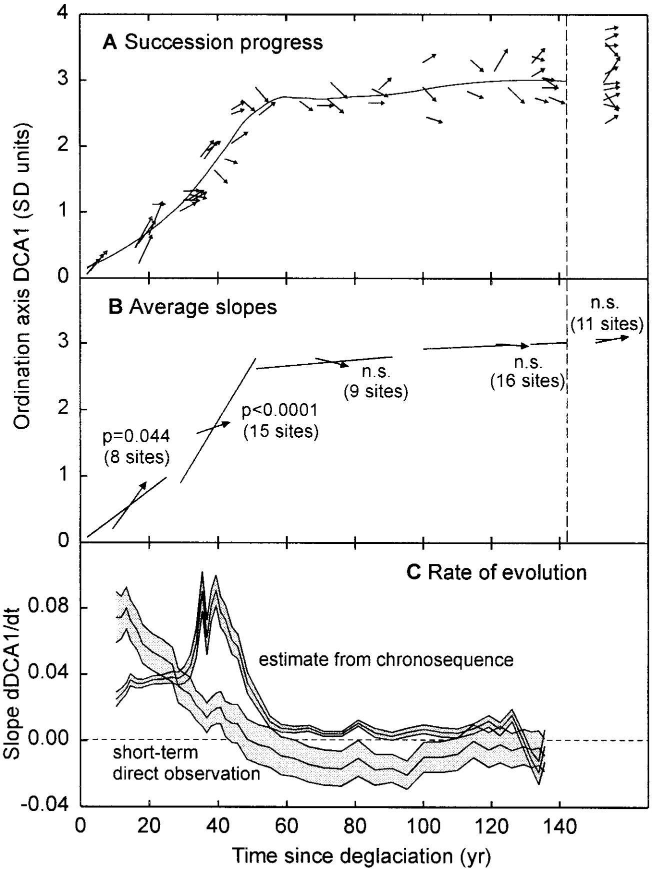

Fig. 1A–C Succession patterns: chronosequence analysis and direct observation. **A** Succession progress with site age. Ordination site scores along the chronosequence (trend line by Loess-smooth) together with average changes observed over 5–6 years (*arrows*). Reference sites adjacent to the glacier foreland are shown to the right of the *broken line* indicating the terminal moraine. **B** Average slopes along the chronosequence (*lines*) and of direct observations (*arrows*) for four age classes (0–30 years, 30–50 years, 50–100 years, >100 years) and for reference sites (>5,000 years). Significances refer to differences between the two slopes. **C** Rates of development (species turnover) reconstructed from the chronosequence and directly observed. Slope estimates ± SE for moving windows of ten consecutive sites along the chronosequence

Short-term rates of change of ordination scores (axis 1) and also of diversity were estimated for each pitfall site by linear regression on year of observation. The smoothed estimates for graphical representation in Fig. 1c and Fig. 3c were obtained from moving windows of ten consecutive sampling sites along the chronosequence. Short-term slopes were estimated by analysis of covariance (common slope for pitfall sites), and the chronosequence trend by regression on age since deglaciation after controlling for the short-term trend (programme STATISTICA 5.5, general linear model module).

For rigorous tests of differences between the short-term changes and the chronosequence trend, the chronosequence was subdivided into four segments for which linear, mixed effects models with maximum likelihood estimation were calculated (site age since deglaciation and year of observation as fixed effects, pitfall site as random factor; calculations done using S-PLUS).

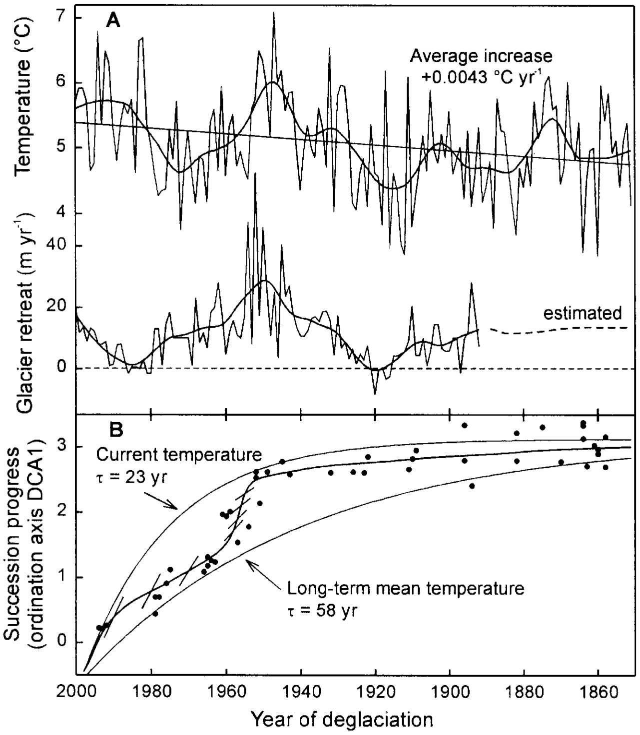

Fig. 2A, B Model relating succession to the climate record. **A** Summer temperature (mean June–September) and retreat of Rotmoos glacier. Temperature record from Vent, adjusted for Rotmoos valley. Glacial retreat prior to 1892 estimated from moraine positions. Smoothed curves used for model calculations. **B** Model fit for succession with rate of development (time constant τ) a function of temperature. Estimate for present appearance of chronosequence (*solid line*) together with currently expected rates of development (*short intersecting lines*). Expected development under constant conditions is shown for the long-term mean temperature and for the current situation with 0.63°C higher temperature (*fine lines*). Data points are ordination site scores (means from 5–6 years of observation)

For model calculations, climate records were smoothed (Loess smooth, see Fig. 2) in order to reduce noise. Numerical integration of the models was done in 1-year steps, implemented as Microsoft Excel spread-sheets using the Solver module for parameter fitting.

Results

Chronosequence and direct observation

Succession progress of communities in relation to age since deglaciation as described by the first axis of Detrended Correspondence Analysis is shown in Fig. 1a together with a smooth trend line. Changes of ordination site scores indicate species turnover; SD units refer to average ranges of species occurrence (tolerance). The change observed over 5–6 years for each sampling site is indicated by arrows (linear regression of yearly ordination site scores vs site age, data points not shown for clarity). The general trend with a rapid evolution of communities over the first 50 years, attaining maximum rates at 30–50 years, and a stagnation of later stages has been described by Kaufmann (2001). Forty-eight sites belonged to the chronosequence; eleven reference sites adjacent to the glacier foreland are shown to the right of the broken line indicating the terminal moraine.

If current evolution of sites were to conform to the chronosequence pattern, yearly site scores would be expected to move along the general trend (Fig. 1a). This, however, was not the case (Fig. 1b). On average the youngest pioneer sites (<30 years) developed slightly faster (P=0.044), and subsequent stages (30–50 years) markedly slower (P<0.001), than expected from the chronosequence approach (significances from linear mixed effects model ANOVA), albeit with considerable variation between individual sites (Fig. 1a). This discrepancy vanished at the older successional stages. The separation into site-age classes was somewhat arbitrary, but was required for stringent statistical tests. In order to illustrate that succession is, in fact, a continuous process I compare in Fig. 1c chronosequence estimates and direct observations of the rate of species turnover on the basis of moving windows of ten consecutive sites along the chronosequence. The currently observed rates of species turnover steadily declined as the final state of succession was attained. No maximum could be observed in the age range 30–50 years as in the reconstruction from the chronosequence. Hints of a slight retrogression at older stages were not statistically significant.

Model for colonisation and climate

Comparing these results with the climate record, both temperature and rate of glacial retreat (Fig. 2a) indicated a connection. A parsimonious model was used for testing plausibility by assuming the final state of succession to be attained asymptotically with a time constant τ under constant conditions as

$$y(t_\mathrm{d}) = 1 - \mathrm{e}^{-t_\mathrm{d}/\tau} \tag{1}$$

with t_d the time since deglaciation and y the successional state given by ordination scores. This corresponds to the differential equation

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \frac{(1-y)}{\tau(T)} \tag{2}$$

Making τ linearly dependent on temperature T with a sensitivity c, allowing further for a delay Δ in the reaction,

$$\tau(t) = \tau_0 - cT(t-\Delta) \tag{3}$$

and integrating over each site's history from deglaciation at t_d until observation at t_o

$$y(t_\mathrm{d}, t_\mathrm{o}) = 1 - \mathrm{e}^{-\int_{t=t_\mathrm{d}}^{t_\mathrm{o}} \frac{1}{\tau(t)}\mathrm{d}t} \tag{4}$$

yields the currently expected state. Figure 2b shows the properly scaled fit of the model using the smoothed tem-

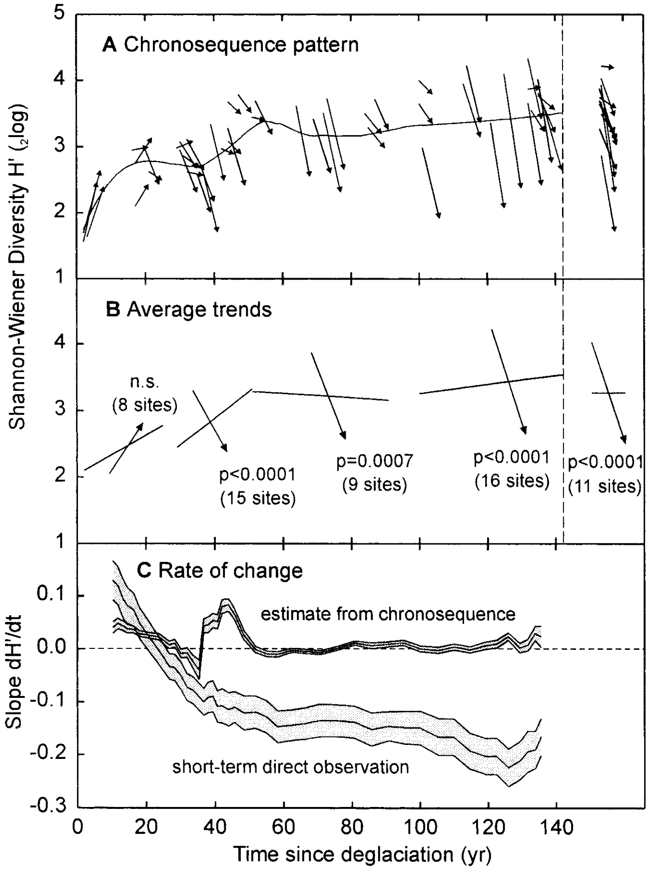

Fig. 3A–C Pattern and change of diversity (analogous to Fig. 1, same statistical assessment). **A** Pattern along chronosequence together with directly observed changes (*arrows*). **B** Average trends of the chronosequence (*lines*) and of direct observations (*arrows*) for four age classes. Significances given for differences between the two slopes. **C** Rates of diversity change reconstructed from the chronosequence and directly observed. Slope estimates ± SE for moving windows of ten consecutive sites along the chronosequence

perature record (Loess-smooth) as the predictor variable *T*. Data points representing site score averages over the observation period are shown together with the model according to Eq. 4 and the expected current rates of change according to Eq. 2.

This model qualitatively reproduced the following most prominent features of my observations: general shape of the chronosequence pattern; higher rates of short-term change at initial stages; lower rates at intermediate stages; and unaltered rates at older sites. The hump in the chronosequence around the 1950 sites appeared to be the result of unusually favourable conditions at this time followed by a cool period.

Considering that the prevailing temperature (mean of last 10 years) is 0.63°C above the long-term average, the model presented in Fig. 2b suggests a severe climate effect on colonisation. A temperature difference of 0.63°C would have more than doubled the initial rate by decreasing the time constant from 58 to 23 years.

Alternative models, either compressing the temperature influence into the very initial stages, or with glacier retreat rates, instead of temperature, being used as the determining factor, described my observations equally well. The latter alternative, in fact, provided the best fit to the currently observed rates of change and it also obviated the need to introduce a reaction delay. However, since temperature is the more fundamental parameter the model used here is based on summer temperatures.

Diversity

Diversity changes along the chronosequence are shown in Fig. 3a–c. The Shannon-Wiener diversity index was analysed in analogy to the ordination scores (Fig. 1). Diversity also showed a hump at the 50-year-old sites which may be a consequence of high temperatures at this time. More conspicuous was the strong decline of diversity during the observation period in all but the initial colonisation stages, not only on the glacier foreland but also at adjacent sites. This amounted to a loss of about 1.5 species per year, out of an average of 22 species per site. This seemingly dramatic reduction in diversity was present in both beetles and spiders, the most species-rich groups. It was not attributable to any specific taxa, but rather occurred among the many rare species. The effect appeared less dramatic when calculated over the entire area, yielding an estimate for species loss of 2% per year which was not statistically significant.

Species counts gave an identical picture to the Shannon-Wiener index, but required a rarefaction technique to correct for varying total catches between years. Due to large scatter and noise the diversity data were less suitable for model calculations than the ordination scores.

Discussion

Environmental factors affecting succession

Obviously temperature is not the only factor to be considered as potentially modifying colonisation and succession, thus leading to a disagreement between chronosequence patterns and direct observation. Moisture in particular has repeatedly been found to modify succession pathways in glacier forelands (Matthews and Whittaker 1987; Kaufmann 2001).

Disturbance such as frequent flooding or ground movement may retard or even preclude succession progress (Zollitsch 1969; Helm and Allen 1995; Kaufmann 2001), resulting in retrogressive development (Matthews and Whittaker 1987). Therefore, sites affected by such disturbance were excluded from the present analysis.

Presence and vicinity of coloniser populations were shown to alter succession pathways in the long (~100 km) succession series at Glacier Bay (Fastie 1995). However, in the small area of Rotmoos valley with all species present in the immediate surroundings this should have less influence considering the high mobility of most invertebrates.

It was argued that the chronosequence approach in succession studies has an advantage over direct observation in that it yields a more integrated picture less influenced by short-term fluctuations (Foster and Tilman 2000). This is obviously true, but, as shown here, precisely these fluctuations may allow us to extract additional information from the chronosequence.

Modelling and explanations

The model proposed here linking the rate of successional evolution to temperature is likely to be oversimplified. Indeed there are indications that colonisation does not immediately start off at its full rate. Moreover, as indicated by more advanced communities at warm, sun-exposed sites on the orographic right side of the valley, the end-point of succession may also depend on temperature (Kaufmann 2001). However, in order to avoid overfitting it seemed reasonable to stick to a strictly parsimonious model with the current data set. Only continued observations can provide further detail.

Whatever the details of the model, the suggested climate effect would be severe and act most strongly on the early colonising stages. Thus, initial communities with low diversity and rapidly changing species composition appeared to be more sensitive to environmental change than more diverse and already structured older communities.

Both direct and indirect effects of temperature have to be considered for possible explanations. As a direct effect, elevated summer temperatures would increase metabolic rates and possibly also mobility. However, an excessive effect of a 0.6°C warming such as observed here seems unlikely. Moreover, a small change in average temperature would not be expected to exert such a strong influence in an environment characterised by large daily temperature fluctuations (up to 40–50°C daily amplitude on the barren surfaces under intense sun irradiation).

No influence of winter temperatures could be detected. This was in agreement with expectation, since temperatures are almost constant under snow-pack, only on rare occasions dropping below –5°C (measurements since 1996). Many invertebrates remain active under these conditions (Addington and Seastedt 1999).

I propose two indirect temperature effects as more likely explanations for accelerated colonisation under warmer conditions. Firstly, prolongation of the very short alpine growing season in warm summers may facilitate species invasion. The snow-free period usually lasts 3 months, but may vary by more than 4 weeks. Warm summers are characterised by early snow-melt and little interruption by episodic periods of snowfall which can happen at any time at these altitudes. Late start of snowfall in autumn, however, may be detrimental as it can cause severe frost in soils devoid of insulation.

Secondly, initial colonisation may be influenced by the rate of glacial recession. Disturbance effects in the immediate vicinity of the glacier edge by meltwater, debris deposition, or microclimatic influence would quickly fade away in front of a rapidly receding glacier, thus favouring the start of colonisation. The even better model fit with glacial retreat rates instead of temperature as input variable makes this hypothesis worth considering. Glacier meltback rates are determined by summer temperatures together with winter precipitation. They reacted rather quickly to the high temperatures of the 1950s, whereas the response to the high but strongly fluctuating average summer temperatures since 1980 was much more delayed.

These latter two hypotheses can be tested by future investigations. Considerable experience exists with experimental prolongation of snow-cover by snow fences (Williams et al. 1998), an approach feasible also for the coloniser sites. Glaciers retreat at a wide range of rates, and even in front of a single glacier individual sites with slowly or rapidly increasing distance from the glacier edge may be found. Appropriate selection of such sites would answer the question whether distance to the glacier and disturbance are important factors.

In alpine areas invertebrates have rarely been investigated in the context of climate change. They are often considered inadequate for the purpose due to complicated phenologies and large abundance fluctuations, whereas the mostly long-lived perennial plants exhibit more integrated dynamics. Here the surface-active invertebrates proved to be reliable indicators with highly consistent results from consecutive years. Abundance varied, but small-scale spatial patterns remained sufficiently stable to show systematic trends.

Vegetation data from Rotmoos glacier foreland are currently insufficient for a similar analysis. In consequence it is not yet possible to decide whether faunal or floral data would be more suitable. It is planned to extend the present investigation as a long-term study for such a comparative assessment.

Conclusion

Even if rapid colonisation is favoured by elevated temperatures, there will also be adverse effects. The seemingly dramatic decline in local diversity probably means that these communities are disturbed under the prevailing warm conditions and lose species faster than can be replaced by invasion of better-adapted species. With the information currently available, I would still expect this to be a temporary fluctuation, since the entire area does not show a disturbing species loss.

Ecosystem responses to temperature changes often appear to be well behaved, but nonetheless some processes may be unexpectedly sensitive. This study reinforces the warning that ecosystems may react to global warming in ways difficult to predict whenever such sensitive processes are involved. Monitoring programmes are necessary to compensate for this lack of understanding. As stressed by Bakker et al. (1996) for vegetation, long-term observation not only reveals pathways of successional changes, but also helps to generate hypotheses on the underlying mechanisms.

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