

# Climate change affects colonization dynamics in a metacommunity of three *Daphnia* species

FLORIAN ALTERMATT\*†, V. ILMARI PAJUNEN †‡ and DIETER EBERT\*†

\*Zoologisches Institut, Universität Basel, Vesalgasse 1, CH-4051 Basel, Switzerland, †Tvärminne Zoological Station, SF-10900 Hanko, Finland, ‡Department of Ecology and Systematics, Division of Population Biology, PO Box 65, Biocenter 3 (Viikinkaari), SF-00014 University of Helsinki, Finland

## Abstract

Climate change is expected to alter the range and abundance of many species by influencing habitat qualities. For species living in fragmented populations, not only the quality of the present patches but also access to new habitat patches may be affected. Here, we show that colonization in a metacommunity can be directly influenced by weather changes, and that these observed weather changes are consistent with global climate change models. Using a long-term dataset from a rock pool metacommunity of the three species *Daphnia magna*, *Daphnia longispina* and *Daphnia pulex* with 507 monitored habitat patches, we correlated a four-fold increase in colonization rate with warmer, drier weather for the period from 1982 to 2006. The higher colonization rate after warm and dry summers led to an increase in metacommunity dynamics over time. A mechanistic explanation for the increased colonization rate is that the resting stages have a higher exposure to animal and wind dispersal in desiccated rock pools. Although colonization rates reacted in the same direction in all three species, there were significant species-specific effects that resulted in an overall change in the metacommunity composition. Increased local instability and colonization dynamics may even lead to higher global stability of the metacommunity. Thus, whereas climate change has been reported to cause a unidirectional change in species range for many other species, it changes the dynamics and composition of an entire community in this metacommunity, with winners and losers difficult to predict.

*Keywords:* *Daphnia magna*, dispersal, *D. longispina*, *D. pulex*, global warming, metapopulation, migration, precipitation, rock pool, temperature

Received 2 July 2007; revised version received 24 October 2007 and accepted 29 October 2007

## Introduction

The Earth's climate has changed during the past 100 years on a regional as well as global scale, and models predict continued changes (IPCC, 2001, 2007; Dore, 2005). The observed and predicted changes are attributable to human activities (IPCC, 2001, 2007). Recorded weather trends over the past 100 years and models for the future generally show an increase in temperature and localized precipitation and a higher year-to-year variability in the weather (IPCC, 2001; Dore, 2005). Due to complex physiogeographic interactions and depending on the season, the effects can also be inversed on a temporal or regional scale (IPCC, 2001; Jylhä *et al.*,

2004). Many studies document unidirectional correlations between climate change and biological phenomena such as altered phenologies (usually a shift towards earlier times in the year), shifts in species ranges (usually polewards and/or to higher altitudes), extinctions (due to changes in the habitat or increased stochasticity), altered life histories, community compositions, ecosystem functions, or genetic changes (Parmesan, 1996, 1999; Roy & Sparks, 2000; McLaughlin *et al.*, 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Balanya *et al.*, 2006). Changes in habitat quality have particularly received a lot of attention (Walther *et al.*, 2002), as they have large implications on the future composition of the fauna and flora. Depending on the system and its location, a change in climate can cause improvements, shifts or degradations of habitats, with consequent effects on the species

Correspondence: Florian Altermatt, fax +41 61 267 03 62, e-mail: florian.altermatt@unibas.ch

occurring in these habitats. Species may become locally extinct or colonize new localities (Parmesan *et al.*, 1999; Franco *et al.*, 2006; Wilson *et al.*, 2006). The ability of a species to shift to new locations will depend on its dispersal potential, on the speed of the habitat change, and on the availability of new habitats for colonization (Holt & Keitt, 2000). It is assumed that the availability of new habitats is affected by climate change (Walther *et al.*, 2002), although not the process of dispersal or colonization itself. However, climate change can potentially have a large influence on colonization rate and colonization success itself, especially in species whose dispersal depends on the weather (Clobert *et al.*, 2001). A combined influence of climate change on both habitat availability and dispersal can either increase or decrease the effects of climate change on biological systems (reinforcement) or make the effects less predictable due to interactions. Furthermore, a direct influence of climate change on dispersal and colonization can also make the systems potentially more variable.

Effects of climate change on habitats were most often seen at the borders of species or population ranges, where the highest sensitivity can be expected (Parmesan, 1996; Bohning-Gaese & Lemoine, 2004). On the contrary, for species that occur in spatially structured systems such as metacommunities or metapopulations, climate change might not only affect the borders of a population's range but also entire populations and their interaction between other populations and species (Thomas & Hanski, 2004). Metapopulations are dynamic *per se*; extinction and colonization on a local scale are implicit features of them, as is dispersal (Gonzalez *et al.*, 1998; Hanski & Gaggiotti, 2004). Therefore, metapopulations offer the possibility of studying the effects of climate change on these processes themselves. In metacommunities, colonization and extinction rates are also functions of the presence of other species, creating an additional level of complexity (Leibold & Miller, 2004; Holyoak *et al.*, 2005). Metacommunity theory is mainly directed towards explaining species coexistence. Species-specific changes in dispersal rates may influence community composition through species sorting in local patches and may alter the overall structure of a metacommunity (Leibold & Miller, 2004).

We studied effective dispersal rates and colonization dynamics in a metacommunity of three *Daphnia* species in southwest Finland. There, these species occur in small freshwater rock pools and exhibit such classical metapopulation dynamics as frequent extinctions and colonizations (Levins, 1970; Hanski & Ranta, 1983; Ebert *et al.*, 2001; Pajunen & Pajunen, 2003). Competition takes place between conspecifics but also between allospecifics (Hanski & Ranta, 1983; Bengtsson, 1989). In this system, particularly the small and shallow rock pools

tend to desiccate during warm, dry periods in summer (Ranta, 1979). When pools dry up, all juvenile and adult *Daphnia* in the population die, and only the resting stages survive. These are potential migrants. Resting eggs are exposed to passive dispersal in the sediments of desiccated rock pools (Maguire, 1963; Ranta, 1979; Ebert, 2005; Vanschoenwinkel *et al.*, 2008) and may colonize new habitat patches.

We wanted to test, if climate change has an effect on metapopulation processes within the metacommunity of three *Daphnia* species. We were interested in general trends and in species' specific reactions that could be explained by the species' ecology. Furthermore, we were interested how changes in colonization dynamics influence the metacommunity composition and diversity.

To answer our questions, we studied the colonization dynamics in 507 potential habitat patches over 24 years during which the weather became significantly warmer and drier. We showed that evaporation in rock pools is significantly higher when ambient temperatures are high. During the same 24 years, we found a significant increase in colonization rates in this *Daphnia* metacommunity. We then correlated colonization rates with annual desiccation risk, using temperature and precipitation as approximation for desiccation risk (Linacre, 1977), to provide a mechanistic explanation for the observed changes. We found increased colonization rates after warm and dry summers for all species in this metacommunity. The increase in colonization rates differed significantly among the three species, and species abundance and composition within this metacommunity changed in accordance with colonization rates. With larger year-to-year changes, the system became more dynamic. As climate change is expected to continue (Walther *et al.*, 2002; Jylhä *et al.*, 2004), its influence will continue and may become even more important. To our knowledge, this is the first time that changes in metapopulation processes, as well as metacommunity dynamics and compositions are directly linked to climate change.

## Materials and methods

We studied the influence of the weather and climate change on colonization rates in a metacommunity of the three planktonic crustaceans *Daphnia magna* Straus, *Daphnia longispina* O. F. Müller, and *Daphnia pulex* De Geer (Crustacea: Cladocera) over a period of 24 years (1982–2006). The three species are widely distributed along the coast of the Baltic Sea, inhabiting freshwater rock pools on the Skerry Islands (Lagerspetz, 1955; Ranta, 1979, 1982; Bengtsson & Ebert, 1998; Ebert *et al.*, 2001; Pajunen & Pajunen, 2003).

### Study area

Our study area included 507 freshwater rock pools on 18 islands in the archipelago of southwest Finland at the Tvärminne Zoological Station (59°50'N, 23°15'E). The rock pools are discrete habitat patches for the three species we studied here, and range in size from 10 to 24 000 L (data not shown, but see Pajunen & Pajunen, 2003; Altermatt & Ebert, in review). The typical depth of rock pools ranges between 10 and 30 cm.

All available rock pools were mapped at the beginning of the study and the number of potential habitats stayed constant during the study period. Only very few rock pools might have become unsuitable due to succession, and no new rock pools were created by the postglacial land uplifting during the study period. Practically all islands and the surrounding Baltic Sea in our study area belong to the Tvärminne Zoological Station and are privately protected since 1901. Although some of the islands may have been used for sheep grazing and lumbering until the mid 1940s, neither activity is likely to have interfered with the rock pools, which are located in the shore belt of the islands. From the 1950s onwards, all use of natural resources was ceased, and only natural succession occurred. Therefore, there have been no changes due to human land use since well before our study time.

We measured daily evaporation (in mm) in 17 rock pools on two islands at 23 24-h intervals. The intervals were representatively spread over the period from 31 May to 20 August 2006. All of these rock pools were free of vegetation. In each rock pool, we placed a brick as a constant reference point. Water level was measured manually, and evaporation could be calculated as the difference between two consecutive measurements to the nearest 0.5 mm. We then related the measured daily evaporation in these rock pools with daily ambient temperature data from the local weather station.

### Weather and characteristics of *Daphnia* sp.

We used weather data from a standard weather station of the Finnish Meteorological Institute measured at the Tvärminne Zoological Station (international identification number WMO 05493, national identification number LPNN 0202). The *Daphnia* populations on the studied islands were about 1.5–3.5 km south of the weather station. Daily mean temperature (°C) and daily precipitation (mm rain) were available for the whole study period (1982–2006). A discontinuous snow cover can occur from mid-October until end of April (unpublished data from the local weather station). The growing season is from the beginning of May to the end of

September/mid-October (unpublished data from the local weather station). Local standardized daily evaporation data (mm day<sup>-1</sup>) were not available. Instead, we used Class A pan (USWB) evaporation data measured at Jokioinen Observatorio of the Finnish Meteorological Institute (WMO 02963, LPNN 1201; 60°48'N, 23°30'E). Jokioinen Observatorio is about 100 km north of the Tvärminne Zoological Station. These data were used to compare standardized daily evaporation relative to ambient mean temperature.

*Daphnia* populations appear in May and can subsist throughout the summer. The production of resting stages (ephippia) peaks in June and July (Altermatt & Ebert, in review). After the end of September, the average temperatures drop below 5 °C; *Daphnia* slow down or stop reproduction, and the planktonic phase of the population eventually goes extinct. During winter, the rock pools are frozen, and no planktonic *Daphnia* are found. The populations survive in form of resting eggs. Thus, for this analysis, we only used meteorological data from the biologically relevant summer period (May to September). For each year, we calculated the average daily temperature from 1 May until 30 September, and the total summer precipitation (summed over the same period).

Because rock pool *Daphnia* differ both in their biology as well as in habitat processes from conspecific populations in lakes, we thus highlight intrinsic characteristics of these populations. All *Daphnia* populations in the rock pools represent metapopulation systems, with frequent extinction and colonization (Pajunen & Pajunen, 2003). The three species studied here either occur singly or coexist in the same rock pool, although they have slightly different ecological preferences (Pajunen & Pajunen, 2003). They differ in competitive abilities, parasite susceptibilities and life strategies (Hanski & Ranta, 1983; Bengtsson, 1989; Ebert, 2005). On average, *D. magna* occurs in small pools, *D. pulex* in intermediate-sized pools and *D. longispina* in larger pools (Lagerspetz, 1955; Ranta, 1979; Bengtsson, 1988). As these species interact with each other, occur in discrete patches and are linked by migration, they are a good example of a metacommunity (Gilpin & Hanski, 1991; Leibold *et al.*, 2004). All three species reproduce by cyclical parthenogenesis, except for some populations of *D. pulex*, which are obligate parthenogenetic. Cyclical parthenogenesis means that phases of asexual production are intermitted by sexual reproduction. Resting eggs (= ephippia) are usually produced as a result of sexual reproduction. These ephippia can outlast unfavourable conditions such as freezing during winter or desiccation of pools during summer (Ebert, 2005). Due to several hatching stimuli per year, long-lasting resting egg banks are absent (Pajunen & Pajunen, 2003). The

ephippia also serve as dispersal stages that migrate passively either by wind or birds (Maguire, 1963; Ranta, 1979), and they are particularly exposed to migration in desiccated rock pools (see Fig. 2.19 in Ebert, 2005; Vanschoenwinkel *et al.*, 2008). Desiccation of individual rock pools has not been monitored. However, evaporation and subsequent desiccation of pools are directly influenced by temperature and precipitation (Linacre, 1977). Also in the herein studied rock pools, evaporation is higher at warmer temperatures (Fig. 2). Especially shallow pools (10–15 cm deep) may dry up within 2–4 weeks, and will be only refilled after sufficient precipitation (Altermatt & Ebert, in review).

Ephippia can migrate into rock pools that are already inhabited by a conspecific *Daphnia* population (= invasion) or into rock pools that have no conspecific *Daphnia* populations (= colonization). Only the latter is considered in this study. Generally, migration and the absolute number of migrants are difficult to estimate (Turchin *et al.*, 1991; Stenseth & Lidicker, 1992), especially when migrants invade existing populations. However, migration and successful establishment into empty habitat patches (= free of conspecifics) can be easily documented by monitoring available habitat patches. Due to asexual reproduction, large planktonic populations can develop within a few weeks, even in rock pools that were colonized by only one ephippium. Genetic data of populations in newly colonized rock pools suggest that most rock pools are colonized by a single or very few individuals (Haag *et al.*, 2005). This may be followed by an influx of further immigrants over time. The survival of a population in a rock pool ranges from less than a year to more than 20 years (Pajunen & Pajunen, 2003). Populations go extinct for various reasons. The most common causes are when rock pools get washed out by waves from the surrounding Baltic Sea (Pajunen & Pajunen, 2003), parasite epidemics (Ebert, 2005), competition with other *Daphnia* species (Bengtsson, 1989) and changes in habitat qualities. Contrary to colonizations, which we expect to increase in parallel to the increase in pool desiccation, we have no predictions about extinctions in the context of a warmer and drier climate.

#### Data collection and analysis

One study author (V. I. P.) visited all 507 rock pools in the study area twice a year from 1982 to 2006 (for detailed methodology, see Pajunen, 1986; Pajunen & Pajunen, 2003). Dry pools, as well as pools filled with water can be colonized, although colonization can only be detected with our method when water is present. Thus, the two yearly samplings did only take place

during periods when all rock pools contained water and when planktonic populations could be detected. In between the samplings, pools may have become desiccated and refilled with water again, especially in warm and dry summers. During each visit, presence or absence of each of the three *Daphnia* species was determined for each pool, yielding the number of populations per year. Yearly population numbers for these three species differ somewhat from the values in Pajunen & Pajunen (2003) due to some corrections in the raw data. The number of populations in a specific year consists of the number of populations in the previous year minus extinctions plus colonizations. From these data, we calculated the number of colonizations and colonization odds. Colonization was defined as the occurrence of a *Daphnia* population in a rock pool where this species had not been observed in the two previous samplings (as defined in Pajunen, 1986; Ebert *et al.*, 2001). Thus, colonizations could only be calculated from the third sampling onwards (meaning from 1983 onwards; no calculations concerning colonizations could be made for the starting year 1982, see also Pajunen & Pajunen, 2003). As a conservative practice to avoid false-positive records, a single negative observation in a series of positive records was not considered as extinction followed by colonization (analogous to Pajunen, 1986; Ebert *et al.*, 2001; Pajunen & Pajunen, 2003). Colonization odds are the number of available empty habitats that were colonized divided by those that were not colonized. For example, if there were 100 available habitats and 20 of these got colonized, colonization odds were as follows:  $20/80 = 0.25$ . This represents a relative measurement of dispersal (also referred to as colonization rates) and not an absolute number of colonizations, as colonization odds are independent of the number of inhabited patches. Available habitats consisted of all monitored rock pools that had not been inhabited by conspecifics in the two previous samplings. Colonization odds reflect the magnitude of dispersal better than the absolute numbers of colonizations, as the latter number might level off when only few empty patches are available. For all three species, we used the colonization odds of rock pools free of these species as a response variable in the later models and in the figures.

Community diversity in the metacommunity was calculated with the Shannon diversity index  $H$  for each year (Zar, 1999). The Shannon diversity index gives the distribution of observations among nominal categories (Zar, 1999). We categorized each inhabited pool on a nominal scale into one of the seven categories of all possible community compositions (the seven categories were the three-species community *D. magna*/*D. pulex*/*D. longispina*, the two-species communities *D. magna*/*D.*

*pulex*, *D. magna*/*D. longispina* and *D. pulex*/*D. longispina* or the one-species communities *D. magna* alone, *D. pulex* alone and *D. longispina* alone). Within these seven categories, the proportion of observations found in each category was used to calculate  $H$ . It should be noted that we calculated the diversity at the community level and not at the species level. A low  $H$  value represents a high probability of finding a specific community, while a high value of  $H$  does not and is, therefore, a sign of a high heterogeneity in this metacommunity (Zar, 1999). For example, if in a given year all 70 pools were inhabited by three-species communities *D. magna*/*D. pulex*/*D. longispina*, the diversity measure  $H$  would be 0. If equal proportions of pools would be inhabited by each of the seven communities (i.e. always 10 pools with each of the possible communities), the diversity measure  $H$  would be 1.95, indicating the much higher diversity.

Statistical analyses were performed with R (R Development Core Team, 2007) using the libraries base, date, Hmisc and asuR. We used linear models to analyse the weather data and a nonparametric Spearman rank correlation for the diversity analysis. We compared colonization rates using generalized linear models with a binomial and quasibinomial error distribution respectively and the logit link function. We tested the assumptions of all our models and compared them with alternative models using other error distributions and other link functions. The chosen model was the best one in respect of fulfilling all assumptions. For analysing changes in population numbers over time, we used a generalized linear model with a Poisson error distribution. The response variable was the absolute value difference in number of populations in two consecutive years calculated for each species separately. It is an integrative measurement of the year-to-year dynamics. The intercepts in all generalized linear models were compared at the arithmetic mean value of the explanatory variable to get a meaningful interpretation. We always fitted a generalized linear model with different slopes for each of the three *Daphnia* species and compared it with a simplified model with only one slope; the comparison was based on a  $\chi^2$  distribution (Venables & Ripley, 2002). If model simplification was not appropriate, we used the former, more complex model. The populations over time are time series, and the measurements are not independent. Therefore, we only fit running medians of the odd span as a robust scatter plot smoothing. We calculated the integer width of the median window using the algorithm AS 296 of Härdle & Steiger (1995). It is implemented in the R function `runmed()` to calculate robust median smoothing (R Development Core Team, 2007).

## Results

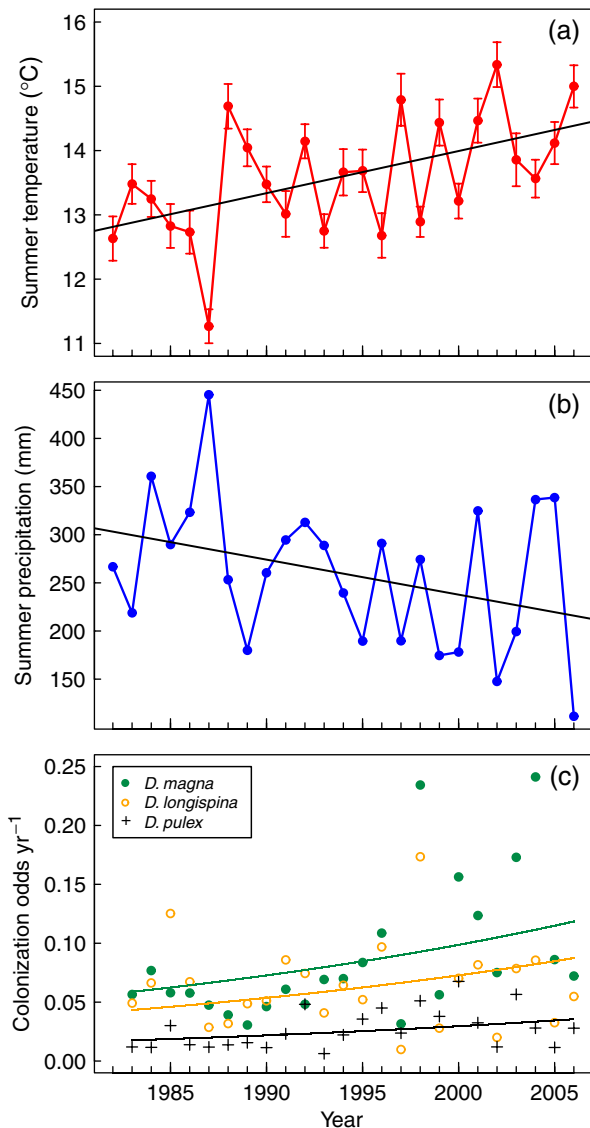
### Weather

At Tvärminne, in the archipelago of southwest Finland, the average summer temperature increased significantly between 1982 and 2006 (linear model,  $R^2 = 0.27$ ,  $F_{1,23} = 8.71$ ,  $P = 0.007$ ,  $N = 25$  years; Fig. 1a). The increase was about 1.6 °C, from 12.8 to 14.4 °C over the 25 years. In parallel, summer total precipitation decreased about 30% (linear model,  $R^2 = 0.12$ ,  $F_{1,23} = 3.16$ ,  $P = 0.08$ ,  $N = 25$  years; Fig. 1b), but showed also a large year-to-year variation. These changes are consistent with global climate change expectations (Walther *et al.*, 2002; Jylhä *et al.*, 2004). Both temperature and precipitation varied highly between different years. Summer average temperature and summer total precipitation were negatively correlated (linear model,  $R^2 = 0.42$ ,  $F_{1,23} = 16.5$ ,  $P = 0.0005$ ,  $N = 25$  years).

In natural rock pools, evaporation per day was significantly positively correlated with the ambient temperature at 23 representative days during summer 2006 (linear model,  $R^2 = 0.27$ ,  $F_{1,21} = 7.7$ ,  $P = 0.01$ ; Fig. 2a). Thus, temperature has a direct impact on evaporation and eventually desiccation. This relation is consistent with standardized evaporation measurements at the weather station: evaporation was also significantly positively correlated with ambient daily temperature over the time period from 1 May to 30 September 1982–2006 (ANCOVA,  $F_{1,3799} = 709$ ,  $P < 0.0001$ ; additionally, there was a significant year-effect,  $P < 0.0001$ ; Fig. 2b). The slope of the correlation from the rock pools (slope = 0.24) did not significantly differ from the slope from the weather station (slope = 0.19; slope-test  $t_{21} = 0.6$ ,  $P = 0.54$ ).

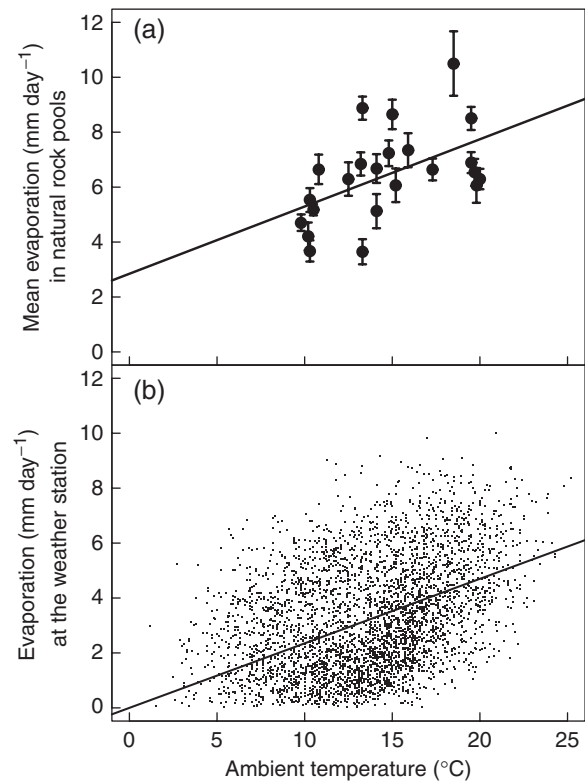
### Colonization

During the study period, 440 out of the 507 available rock pools were inhabited at least once by any of the species (= 87%). In this metacommunity, we observed 763 colonizations of empty habitat patches by *D. magna*, 604 colonizations by *D. longispina* and 284 colonizations by *D. pulex*. In the same time period, colonization rates of the three *Daphnia* species significantly increased (generalized linear model,  $Z = 3.15$ ,  $P = 0.002$ ; Fig. 1c), indicating a relation to climate change. The change of colonization rates did not differ among the three species. Although both the weather and colonization rates changed significantly during the period of 1982–2006, they do not necessarily have to be related. Thus, we additionally tested if colonization rates do not only change over time, but are furthermore, depending directly on the weather. We found that the annual



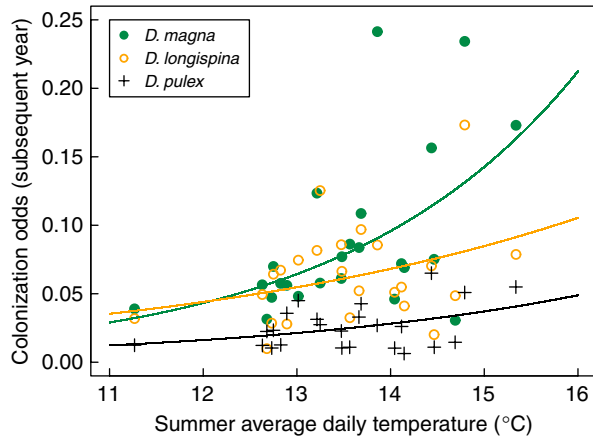
**Fig. 1** Weather data from southwest Finland during the study period from 1982 to 2006 and parallel changes in colonization rates in a metacommunity of three *Daphnia* species. For the weather data, daily weather data from 1 May until 30 September were used for each year. (a) Summer average daily temperature ( $\pm$ SE) increased significantly during this period (black line: least-squares fit,  $P = 0.007$ ). (b) In parallel, there was a marginal significant decrease in summer total precipitation (black line: least-squares fit,  $P = 0.08$ ). (c) Colonization odds in a metacommunity of three *Daphnia* species increased significantly during the same time period ( $P < 0.002$ ). Colonization odds are the number of available empty habitats that were colonized divided by those that were not colonized (see 'Materials and methods'). The lines show estimated values from the generalized linear model fitted for each species.

colonization odds of the three *Daphnia* species correlated significantly positively with average summer temperature and negatively with summer total precipi-

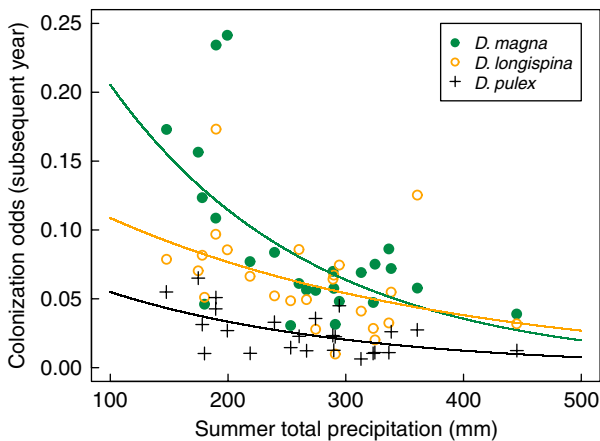


**Fig. 2** Evaporation relative to ambient daily mean temperature. (a) Mean evaporation ( $\text{mm day}^{-1}$ ) in 17 rock pools at 23 representative days during summer 2007. Evaporation was significantly higher at warmer temperatures ( $P = 0.01$ ). The straight line is the mean squares line. (b) Mean evaporation ( $\text{mm day}^{-1}$ ) relative to ambient temperature measured at a standardized weather station. All days from 1 May to 30 September 1982–2006 are included. Evaporation was significantly higher at warmer temperatures ( $P < 0.0001$ ). The straight line is the mean squares line.

tation in the preceding year (Fig. 3). The correlation with precipitation was less pronounced, probably due to the large year-to-year variability. There are not only significant changes in both the weather and colonization rates over time, but furthermore we highlight a significant direct correlation between the weather and colonization rates. Summers with low average daily temperatures were followed by a year with fewer colonizations of all three *Daphnia* species than summers with a high average daily temperature (generalized linear model,  $Z = 4.48$ ,  $P < 0.00001$ ; Fig. 3). The slopes of the curves differed significantly for the three *Daphnia* species (model with separate slopes for each of the *Daphnia* species compared with a model with only one common slope:  $\Delta\text{df} = 2$ ,  $\Delta\text{deviance} = 7.64$ ,  $P = 0.02$ ). Similar results were found when comparing colonization odds and summer total precipitation. Dry summers (low precipitation) were followed by a year with more

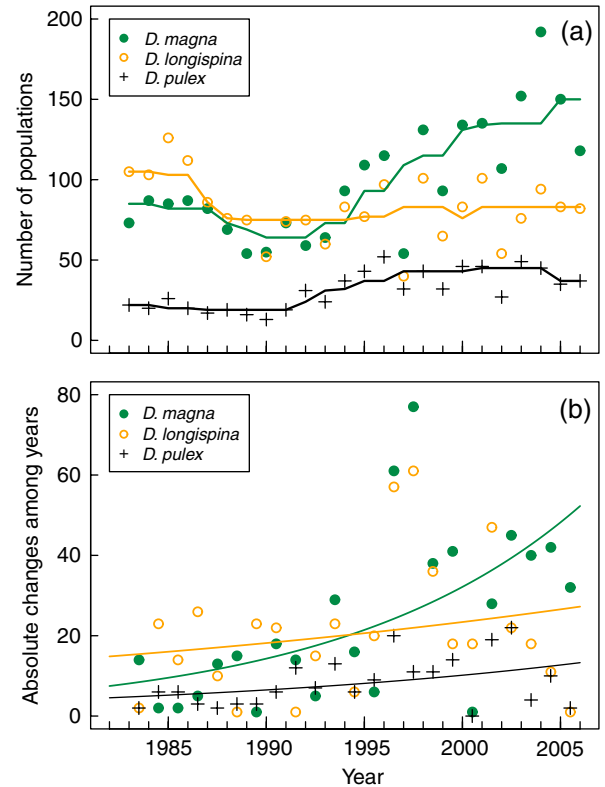


**Fig. 3** Colonization odds of three *Daphnia* species relative to the temperature in the preceding year. There was a significant positive effect of the summer average daily temperature on the colonization odds in the subsequent year ( $P < 0.00001$ ). This effect was significantly different for the three *Daphnia* species ( $P = 0.02$ ). The lines show estimated values from the generalized linear model fitted for each species.



**Fig. 4** Colonization odds of three *Daphnia* species relative to the total precipitation in the preceding year. There was a significant negative effect of the summer total precipitation on the colonization odds in the subsequent year ( $P < 0.00001$ ). The effect was significantly different for the three *Daphnia* species ( $P = 0.02$ ). The lines show estimated values from the generalized linear model fitted for each species.

colonizations of all three *Daphnia* species than wet summers (generalized linear model,  $Z = -5.61$ ,  $P < 0.00001$ ; Fig. 4). Again, the three *Daphnia* species reacted differently, and the slopes of the species' curves differed (model with separate slopes for each of the *Daphnia* species compared with a model with one common slope:  $\Delta df = 2$ ,  $\Delta deviance = 7.62$ ,  $P = 0.02$ ). Thus, *Daphnia* colonization rates increased after both dry and warm summers, and this effect varied across

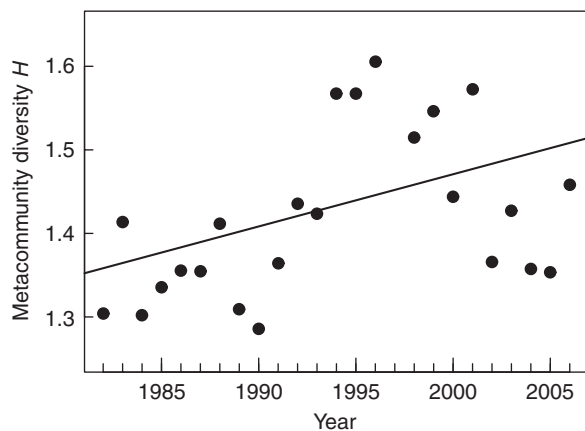


**Fig. 5** (a) Number of populations of three different *Daphnia* species within a metacommunity with 507 available habitats during 1982 and 2006. The species both occurred separately or coexisted in the same rock pools. The lines show separate running medians for the three species. (b) The same data, but now absolute changes in populations' number between two consecutive years are shown for each species. There was a significant increase in the year-to-year variation in number of populations, and thus the metacommunities became more dynamic over time ( $P < 0.0003$ ; generalized linear model, see 'Materials and methods'). The lines show estimated values from the generalized linear model fitted for each species.

species. Summers are getting warmer and drier due to climate change (Fig. 1a and b). Therefore, climate change has a direct influence on colonization dynamics (Figs 1c, 2 and 3) in this metacommunity.

*Community composition*

Looking at the weather changes from 1982 to 2006 together with the correlation between colonization rates and weather phenomena in three *Daphnia* species, one can expect to see temporal effects in the composition of this metacommunity. First, the number of populations per year changed for each of the species over the study period (Fig. 5a). Interestingly, while all species had higher colonization rates consistent with local climate change, the number of populations developed



**Fig. 6** The metacommunity diversity (Shannon index) increased significantly over time ( $P = 0.012$ ). Annual composition of the metacommunity was analysed by categorizing each inhabited pool into seven categories on a nominal scale (three one-species categories, three two-species categories and one three-species community). Thereof the overall community diversity was calculated (black line: least-squares fit for illustration).

differently for each of the three species. In this metacommunity, the number of *D. magna* and *D. pulex* populations doubled over the study period, while the number of *D. longispina* populations decreased over time (Fig. 5a). Second, our data suggest that this metacommunity became more dynamic in recent years (Fig. 5b). There was a significant increase in absolute value changes for all species among consecutive years over time (1982 to 2006; generalized linear model,  $Z = 3.6$ ,  $P = 0.0003$ ). However, the magnitude of this effect differed significantly among the three species and the increase was most pronounced in *D. magna* (model with separate slopes for each of the *Daphnia* species compared with a model with one common slope:  $\Delta df = 2$ ,  $\Delta deviance = 32.6$ ,  $P < 0.0001$ ; Fig. 5b). It is, therefore, possible that climate change did not only influence colonization rates, but especially in *D. longispina* also extinction rate, as losses in the number of populations are included in the absolute changes. When considering community composition as species interactions (namely the possibility of multi-species communities), we found that diversity in the metacommunity increased significantly over time ( $R_S = 0.50$ ,  $n = 25$ ,  $P = 0.012$ ; Fig. 6). Overall, the whole metacommunity became more dynamic and more diverse.

## Discussion

In southwest Finland, the summer temperature significantly increased and precipitation decreased between 1982 and 2006, which is in accordance with the global climate change (Fig. 1a and b). Changes in precipitation

are known to be more variable and less pronounced than the changes in temperature in all climate change models (Walther *et al.*, 2002; Jylhä *et al.*, 2004). In Northern Europe, annual precipitation is predicted to increase (Jylhä *et al.*, 2004; Zhang *et al.*, 2007) due to an increase during the winter. However, precipitation is predicted to decrease or stay constant over the summer (Jylhä *et al.*, 2004), and this is also evident in our data (Fig. 1b). Over the summers, we found a highly significant increase in mean temperature, but only a marginal significant decrease in precipitation, with a large year-to-year variation in precipitation. During the same time period, an increase in colonization rates for all *Daphnia* species (Fig. 1c), species-specific changes in colonization rates and changes in the metacommunity composition were found (Fig. 5). Colonization rates in *Daphnia* metapopulations were significantly higher after warm and dry summers and the magnitude of the effect differed for the three species. A mechanistic explanation for these findings is that evaporation in rock pools is positively correlated with the ambient temperature (Fig. 2a). Pools dry up more rapidly during warm, dry periods, and ephippia get exposed to dispersal by wind and bird (Maguire, 1963; Ranta, 1979; Ebert, 2005). The species-specific reaction changed the absolute numbers of populations and made the whole metacommunity more dynamic. Along with many documented changes in habitat availability due to climate change (Walther *et al.*, 2002), this is the first time that changes in metapopulation processes, metacommunity composition and dynamics themselves can be related to climate change.

### Temporal trends of the weather

It is generally accepted that annual mean temperature and precipitation are influenced by climate change in Northern Europe (IPCC, 2001; Jylhä *et al.*, 2004). Whereas temperature is predicted to increase in all seasons, precipitation trends differ among seasons. We, therefore, restricted our comparisons to the time period of *Daphnia* growth (i.e. May to September), when precipitation is either predicted to stay constant (Jylhä *et al.*, 2004) or decrease (Walther *et al.*, 2002). The significant increase in temperature and the marginal significant decrease in precipitation in our weather data from the Tvärminne Zoological Station are in accordance with these predictions (Fig. 1a and b).

### Evidence for weather-driven changes in colonization rates

Metapopulations and metacommunities are predisposed for the study of colonization and extinction (Hanski & Gaggiotti, 2004). Colonization is an intrinsic



process in these systems, and metapopulations also explicitly integrate the fact that the distribution of suitable habitats does not remain constant through time (Hanski & Gaggiotti, 2004; Thomas & Hanski, 2004). Species in metapopulations have prerequisites to deal with the dynamic availability of habitats, and colonization–extinction processes are thought to be under selection (Hanski & Gaggiotti, 2004).

In a metacommunity of three different *Daphnia* species, we found a correlation between colonization rates and weather in the previous season. The occurrence and timing of rock pool desiccation varied widely between the years and among pools (Pajunen & Pajunen, 2003; Ebert, 2005). Daily evaporation is correlated with ambient temperature (Fig. 2), and desiccation depends on the depth of rock pools (Ebert *et al.*, 2001). In desiccated pools, ephippia are more exposed to dispersal by wind and birds (see Fig. 2.19 in Ebert, 2005). Thus, the strength of a drought determines which pools will be potential sources of migrants, as medium-sized pools, for example, may only contribute migrants during longer droughts. In the context of climate change, summer weather will change in a direction that increases migration in this metacommunity.

In all three species, not only the dispersal but also the production of ephippia might be influenced in the same direction by the weather. Ephippia are produced continuously during the summer, and populations in small pools produce large numbers of ephippia (Altermatt & Ebert, in review). The continuous production of large numbers of ephippia in small pools may even be an adaptation in such dynamic habitats, as it guarantees long-term survival in semistable habitats. Warm water temperatures stimulate population growth, and the production of ephippia peaks in mid-summer when droughts are also occurring (Altermatt & Ebert, in review). Genetic data suggest that there are usually one to two colonizers in a newly colonized rock pool (Haag *et al.*, 2005, 2006). It is, therefore, likely that populations in the most newly colonized rock pools resulted from one successfully colonized ephippium, containing one or two eggs. Due to asexual reproduction, even a single colonizer might have established a planktonic population in the same year or in the next spring and was detected by our sampling scheme. Given a causal relationship between temperature/precipitation and colonization, we expect even more dispersal and colonizations in the future due to climate change, and that the additional desiccated pools will become sources of migrants. Parallel to new colonizations, migration into existing populations (= invasion) is expected to increase. This will influence the genetic structure of the resident population (Ebert *et al.*, 2002; Haag *et al.*, 2005), affect local adaptation of parasites

(Altermatt *et al.*, 2007) and parasite dispersal itself (Ebert *et al.*, 2001): newly colonized and short-lived host populations may be more inbred and have less parasites, and there may also be disturbed dynamics in host–parasite coevolution within populations.

We already have good indications that between-population dynamics in this metacommunity increased, as we found that absolute changes in annual population numbers increased in parallel to the ongoing climate change (Fig. 5b). This effect was most pronounced in *D. magna*. One possible explanation could be that a higher colonization rate after warm and dry summers leads to the colonization of habitats where either suboptimal abiotic factors or increased allospecific competition is present. This occupancy of suboptimal habitats could result in short-term occupancy followed by local population extinctions. The different trends in number of populations per year (Fig. 5a) must be due to changes in the colonization–extinction balance or colonization–extinction trade-offs (Hanski & Ranta, 1983; Calcagno *et al.*, 2006). While *D. magna* and to some extent also *D. pulex* can actually increase the number of populations in parallel with the increase in colonizations, *D. longispina* does not become more frequent over time even though its colonization rate is increasing as well. It suggests that in *D. longispina* a trade-off exists. Warmer and drier weather will benefit colonization, but could reduce survival of populations. This could be due to aspects of that species' biology, as preferences for large pools with low salinity (Ranta, 1979).

In our study area, we can exclude changes in habitat patch numbers and human activities as alternative explanation for the changes in colonization dynamics (see 'Materials and methods' for details). This is an advantage of our data, as in many other studies the influence of climate change is strongly confounded by anthropogenic habitat changes (Warren *et al.*, 2001; Walther *et al.*, 2002), complicating the separation of these forces. Also, within all monitored rock pools, the number of available empty rock pools (= free of a specific species' population) always outnumbered the inhabited rock pools by a factor of 2–10, depending on the species and the year (Fig. 5a). Thus, the availability of empty rock pools seemed not to be a limiting factor.

#### *Species' specific effects alter the metacommunity composition*

Colonization rates relative to weather in the previous year differed significantly among the three *Daphnia* species (Figs 3 and 4). At the same time, we observed a change in species abundances within the metacommunity whereby *D. magna* became more abundant

(Fig. 5a and b) and an increase in the metacommunity diversity (Fig. 6). Increased local instability and colonization dynamics may even lead to higher global stability of the metacommunity. The link between the individual changes in the three-species populations and the increase in the metacommunity diversity is not compulsory (Holyoak *et al.*, 2005): the three species could increase their population numbers in separate pools. Pool occupancy is still far from saturation.

Metacommunity diversity includes the occurrence of all seven possible species communities in each rock pool at any time. Although the three *Daphnia* species are competitors (Bengtsson, 1989), the increased colonization dynamics resulted in a higher number and diversity of multi-species communities (Holyoak *et al.*, 2005) and not in monopolizations of habitats (Fig. 6). This supports the hypothesis of Hanski & Ranta (1983) that coexistence of the three ecologically similar species is possible due to the patchy distribution and metapopulation dynamics.

Immigration into already existing populations is generally more complex than colonization of empty habitat patches. The existing populations numerically dominate the immigrants (De Meester *et al.*, 2002), which makes immigration difficult. Although, the presence of parasites (Altermatt *et al.*, 2007) or predators (Ranta, 1982) may increase the immigration success. Even though predators as dytiscids or corixids may have an influence on population densities, they are not capable of driving populations to extinction (Pajunen & Pajunen, 2003).

Hanski & Ranta (1983) suggested that *D. magna* is the best colonizer but worst competitor, *D. longispina* the best competitor but worst colonizer and *D. pulex* intermediate. This hypothesis could not be confirmed on the basis of genetic data (Haag *et al.*, 2006). We do not make direct statements on the colonization and competitive abilities for these three species, but rather on relative changes in colonization processes over time. However, our data are consistent with the idea that *D. magna* is a good colonizer (Hanski & Ranta, 1983), as its colonization rates were highest and it profited most from the warmer weather. Nevertheless, it does not replace the other two species, indicated by an increasing diversity of pool communities (Fig. 6). This shows that it either colonizes only previously empty habitats, or pools already inhabited by allospecific *Daphnia* without driving them to extinction.

The species-specific colonization rates can in part be explained by the dispersal strategies and the known habitat preferences of these species. First, the range of possible habitats is large, although only *D. magna* favours or can handle more saline habitats (Lagerspetz, 1955; Bengtsson, 1988). *D. magna* also occurs more often

in smaller pools, while *D. pulex* is more often found in intermediate-sized pools and *D. longispina* in large pools (Lagerspetz, 1955; Ranta, 1979; Bengtsson, 1988). Warm, dry summers create the type of habitat that is favoured by *D. magna*: water volume is smaller and evaporation leads to higher salinity. Ehippia in small pools get exposed more often during dry periods. Indeed, the colonization rate of this species not only increased after warm summers but its population numbers also doubled within the metapopulation over the 24 years. On the contrary, *D. longispina* prefers larger rock pools with low salinity (Lagerspetz, 1955; Ranta, 1979; Bengtsson, 1988) and *D. pulex* has intermediate preferences. Large rock pools with lower salinity may be more available during cooler and wet summers (also less evaporation), and are also less vulnerable to desiccation (Ranta, 1979). Second, the ehippia of the three species differ morphologically (Hanski & Ranta, 1983). Only ehippia from *D. magna* have long pennate appendages that might facilitate their dispersal either by wind or birds (Hanski & Ranta, 1983). We speculate that *D. magna* had the largest response in colonizations after warm and dry years, because this species combines these two characteristics that could favour dispersal from desiccated pools. Furthermore, an increased colonization rate in one species could influence allospecific colonizations, as priority effects or changes in competition–colonization balances may occur (Hanski & Ranta, 1983).

### Conclusions

A rapid and directed climate change is occurring due to human activities. We found correlative evidence that colonization rates in a metacommunity of three *Daphnia* species are higher after warm, dry summers, and that these weather conditions are becoming more frequent due to climate change. A mechanistic explanation for the increased colonization rates is that resting stages in dry pools are more exposed to wind and animal dispersal. Some species profited more, in respect to colonization, from warm, dry weather and their number of populations increased. When individual species colonized habitat patches that were already inhabited by allospecific *Daphnia*, the whole metacommunity got more diverse. Thus, climate change not only increased the dynamics in the system but also altered metacommunity composition itself.

### Acknowledgements

We thank M. Reinikainen from the Tvärminne Zoological Station and the Finnish Meteorological Institute for weather data, T. Fabbro for help with the statistical analyses, T. Zumbrohn

for help during the preparation of the raw data, O. Balmer, D. Brites, S. Gaba and L. Mouton for discussions and S. Zweizig and three anonymous reviewers for comments on the manuscript. The study was supported by the Swiss National Science Foundation. F. A. thanks the Basler Stiftung für experimentelle Zoologie, the Freiwillige Akademische Gesellschaft and the Emilia Guggenheim-Schnurr-Stiftung for financial support during the fieldwork. This work is part of project no. 97524006 at the Tvärminne Zoological Station.

## References

- Altermatt F, Ebert D (in review) The influence of habitat size and stability on the production of migrants in a *Daphnia magna* metapopulation. *Oecologia*.
- Altermatt F, Hottinger J, Ebert D (2007) Parasites promote host gene flow in a metapopulation. *Evolutionary Ecology*, **21**, 561–575.
- Balanya J, Oller JM, Huey RB, Gilchrist GW, Serra L (2006) Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science*, **313**, 1773–1775.
- Bengtsson J (1988) Life histories, interspecific competition and regional distribution of three rockpool *Daphnia* species. *Acta Universitatis Upsaliensis*, **142**, 1–32.
- Bengtsson J (1989) Interspecific competition increases local extinction rate in a metapopulation system. *Nature*, **340**, 713–715.
- Bengtsson J, Ebert D (1998) Distribution and impacts of micro-parasites on *Daphnia* in a rockpool metapopulation. *Oecologia (Berlin)*, **115**, 213–221.
- Bohning-Gaese K, Lemoine N (2004) Importance of climate change for the ranges, communities and conservation of birds. *Advances in Ecological Research*, **35**, 211–236.
- Calcagno V, Mouquet N, Jarne P, David P (2006) Coexistence in a metacommunity: the competition–colonization trade-off is not dead. *Ecology Letters*, **9**, 897–907.
- Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) (2001) *Dispersal*. Oxford University Press, Oxford.
- De Meester L, Gomez A, Okamura B, Schwenk K (2002) The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecologica – International Journal of Ecology*, **23**, 121–135.
- Dore MHI (2005) Climate change and changes in global precipitation patterns: what do we know. *Environment International*, **31**, 1167–1181.
- Ebert D (2005) *Ecology, Epidemiology, and Evolution of Parasitism in Daphnia*. National Library of Medicine (US), National Center for Biotechnology Information, Bethesda, MD.
- Ebert D, Haag C, Kirkpatrick M, Riek M, Hottinger JW, Pajunen VI (2002) A selective advantage to immigrant genes in a *Daphnia* metapopulation. *Science*, **295**, 485–488.
- Ebert D, Hottinger JW, Pajunen VI (2001) Temporal and spatial dynamics of parasites in a *Daphnia* metapopulation: which factors explain parasite richness? *Ecology*, **82**, 3417–3434.
- Franco AMA, Hill JK, Kitschke C *et al.* (2006) Impacts of climate warming and habitat loss on extinctions at species' low-altitude range boundaries. *Global Change Biology*, **12**, 1545–1553.
- Gilpin M, Hanski I (eds) (1991) *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London.
- Gonzalez A, Lawton JH, Gilbert FS, Blackburn TM, Evans-Freke I (1998) Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, **281**, 2045–2047.
- Haag CR, Riek M, Hottinger JW, Pajunen VI, Ebert D (2005) Genetic diversity and genetic differentiation in *Daphnia* metapopulations with subpopulations of known age. *Genetics*, **170**, 1809–1820.
- Haag CR, Riek M, Hottinger JW, Pajunen VI, Ebert D (2006) Founder events as determinants of within-island and among-island genetic structure of *Daphnia* metapopulations. *Heredity*, **96**, 150–158.
- Hanski I, Gaggiotti OE (eds) (2004) *Ecology, Genetics and Evolution of Metapopulations*. Elsevier Academic Press, Amsterdam.
- Hanski I, Ranta E (1983) Coexistence in a patchy environment: three species of *Daphnia* in rock pools. *The Journal of Animal Ecology*, **52**, 263–279.
- Härdle W, Steiger W (1995) Optimal median smoothing. *Applied Statistics*, **44**, 258–264.
- Holt RD, Keitt TH (2000) Alternative causes for range limits: a metapopulation perspective. *Ecology Letters*, **3**, 41–47.
- Holyoak M, Leibold MA, Holt RD (eds) (2005) *Metacommunities. Spatial Dynamics and Ecological Communities*. The University of Chicago Press, Chicago.
- IPCC (2001) *Climate Change 2001: The Scientific Basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis. Summary for Policymakers*. WMO and UNEF, Geneva.
- Jylhä K, Tuomenvirta H, Ruosteenoja K (2004) Climate change projections for Finland during the 21st century. *Boreal Environment Research*, **9**, 127–152.
- Lagerspetz K (1955) Physiological studies on the brackish water tolerance of some species of *Daphnia*. *Archivum Societatis Zoologicae Botanicae Fennicae Vanamo*, **9** (Suppl.), 138–143.
- Leibold MA, Holyoak M, Mouquet N *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.
- Leibold MA, Miller TE (2004) From metapopulations to metacommunities. In: *Ecology, Genetics and Evolution of Metapopulations* (eds Hanski I, Gaggiotti OE), pp. 133–150. Elsevier Academic Press, Amsterdam.
- Levins R (1970) Extinction. *Lecture Notes in Mathematics*, **2**, 75–107.
- Linacre ET (1977) A simple formula for estimating evaporation rates in various climates, using temperature data alone. *Agricultural Meteorology*, **18**, 409–424.
- Maguire B (1963) The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecological Monographs*, **33**, 161–185.
- McLaughlin JF, Hellmann JJ, Boggs CL, Ehrlich PR (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Science*, **99**, 6070–6074.
- Pajunen VI (1986) Distributional dynamics of *Daphnia* species in a rock-pool environment. *Annales Zoologici Fennici*, **23**, 131–140.

- Pajunen VI, Pajunen I (2003) Long-term dynamics in rock pool *Daphnia* metapopulations. *Ecography*, **26**, 731–738.
- Parnesan C (1996) Climate and species' range. *Nature*, **382**, 765–766.
- Parnesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- R Development Core Team (2007) *R: A Language and Environment for Statistical Computing. Version 2.4.0*. R Foundation for Statistical Computing, Vienna, Austria.
- Ranta E (1979) Niche of *Daphnia* species in rockpools. *Archiv für Hydrobiologie*, **87**, 205–223.
- Ranta E (1982) Animal communities in rockpools. *Annales Zoologici Fennici*, **19**, 337–347.
- Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.
- Stenseth NC, Lidicker WZ (eds) (1992) *Animal Dispersal. Small Mammals as a Model*. Chapman & Hall, London.
- Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thomas CD, Hanski I (2004) Metapopulation dynamics in changing environments: butterfly responses to habitat and climate change. In: *Ecology, Genetics and Evolution of Metapopulations* (eds Hanski I, Gaggiotti OE), pp. 489–514. Elsevier Academic Press, Amsterdam.
- Turchin P, Odendaal FJ, Rausher MD (1991) Quantifying insect movement in the field. *Environmental Entomology*, **20**, 955–963.
- Vanschoenwinkel B, Gielen S, Seaman M, Brendonck L (2008) Any way the wind blows – frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos*, **117**, 125–134.
- Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York.
- Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Warren MS, Hill JK, Thomas JA *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2006) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138–1146.
- Zar JH (1999) *Biostatistical Analysis*, 4th edn. Prentice-Hall, London.
- Zhang X, Zwiers FW, Hegeri GC *et al.* (2007) Detection of human influence on twentieth-century precipitation trends. *Nature*, **448**, 461–466.