Hierarchical models for describing space-for-time variations in insect population size and sex-ratio along a primary succession

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ABSTRACT

Chronosequences of glacier retreat are useful for investigating primary successions over time periods that are longer than direct observation would permit. In this context, space-for-time substitution studies have been applied to assess the effects of climate change on invertebrate assemblages. However, population dynamics of insect species following retreating glaciers has been under-investigated until now due to difficulty in applying capture-recapture methods and correctly identifying species in the field. Removal sampling methods are commonly used, but imperfect detectability is rarely accounted for in the analytical framework. In this paper we study the effects of environmental drivers of spatial, and indirectly temporal, variation in population size and sex-ratio of cold-adapted insects through a hierarchical framework for abundance. We show the importance of a metapopulation design, where samples are replicated in space and time, to model data from small and scattered populations, typically present in habitats with climate-mediated selective pressure like those along glacier forelands. This scattered distribution can influence the observation or sampling process and thus species detectability.

Our results show that glacier retreat differently affects species-specific changes of population size and sex ratio along the chronosequence, even if the species are taxonomically related. Small-sized populations occur on the glacier surface, near the glacier front, and in sites deglaciated for at least 100 yrs. On the contrary, larger populations occupy sites deglaciated for more than 20 yrs, but less than 100 yrs. This pattern is described by the concave relationship of abundance with both species richness of other arthropods (proxy of habitat complexity) and soil organic matter (proxy of soil maturity). Sex-ratio showed opposite patterns in relation to time since deglaciation. Hierarchical models that estimate abundance of spatially distinct subpopulations represent useful tools for accurately assessing changes in species abundance following climate change while accounting for possible bias associated with imperfect detectability, an issue which is often neglected in space-for-time substitution studies on invertebrates and, more generally, in studies involving pitfall trapping.

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1. Introduction

In recent years, many studies have described and quantified changes in animal communities in response to climate change (e.g. Parmesan, 2006; Bellard et al., 2012). Space-for-time substitution studies and investigations of chronosequences have been used to understand climate-driven changes in biodiversity (Guisan and Thuiller, 2005). In particular, along a retreating-glacier foreland the use of the chronosequence as a space-for-time substitution (Walker et al., 2010) has provided significant insights into insect community dynamics or trophic networks (Kaufmann, 2001; Hodkinson et al., 2002; Gobbi et al., 2007; Losapio et al., 2015). On the contrary, very little is known about spatial and temporal changes in population size and structure (e.g. sex-ratio) of species living in areas left behind by retreating glaciers and on the glacier surface.

Glacier forelands, which are represented by terrains freed by the retreating glaciers, are characterised by a well-known chronosequence of glacial recession which makes them a relatively

artifact-free system for studying insect colonisation dynamics (primary successions). Plots of different ages are presumed to represent different stages of development of the actual succession, with a dated initial colonisation (early successional stages) and a known history afterwards (mid- and late-successional stages) (Matthews, 1992; Bardgett et al., 2005). These chronosequences thus allow the investigation of ecological processes over time periods that are longer than direct observation would permit (Walker et al., 2010) and can be used to investigate the effects of climate change on the dynamics of population size and structure.

When estimating abundance of insect populations we need to account for the fact that individuals cannot be observed perfectly (i.e. detection probability $p < 1$) using practical sampling strategies and that imperfect detection can induce important bias in abundance estimates of wild species (e.g. Williams et al., 2002). Despite that, imperfect detection is rarely accounted for in studies on insect communities and populations (Kellner and Swihart, 2014) like those involving space-for-time substitution and chronosequences to evaluate climate change effects on population dynamics. In addition, the quantitative nature of pitfall traps has been debated arguing that the number of individuals sampled is a function of both population size and species activity on the ground (Leather, 2004). Moreover, in habitats with climate-mediated selective pressure like those along the glacier forelands, insects can be present with small and scattered populations. Thus, trap efficiency and the scattered distribution of species can influence the observation or sampling process and thus species detectability.

Spatially and temporally replicated data are required to directly model patterns of abundance and sex-ratio while accounting for possible distorting patterns in detectability (Royle et al., 2007). Observations from spatially distinct subpopulations can be pooled to infer about metapopulation-level parameters that describe the extent to which abundance and detectability differ among local populations (Royle and Dorazio, 2008). This can be achieved by using recently-developed hierarchical models (Royle and Dorazio, 2006, 2008) where a state-space formulation combines two stochastic components, the ecological process and a conditional observation process. The ecological process describes the spatial (and possibly temporal) variation in abundance, whereas the observation process is a stochastic description of the sampling protocol, such as detection/non-detection, capture-recapture, or removal sampling (Williams et al., 2002). The latter is a well-established procedure for sampling invertebrates and estimating abundance of demographically closed populations, which are sampled on different occasions by physically removing individuals from the population.

In this paper we study the temporal dynamics of ground-dwelling and cold-adapted insect populations in relation to climate change by applying, for the first time, a state-space metapopulation model to a gradient analysis carried out along a chronosequence of glacier retreat. We used cold-adapted insect species as model organisms due to their sensitivity to climate change (Gobbi et al., 2014; Pizzolotto et al., 2014). To our knowledge, this is the first attempt to model changes in detection probability, abundance and sex-ratio of insect species in relation to time since deglaciation. We accomplished this by explicitly testing hypotheses on the abiotic and biotic drivers of detectability, population size and structure along the chronosequence through a Bayesian variable selection approach. Specifically, we tested for each species whether (a) detection probability was affected by habitat characteristics along the chronosequence, (b) changes in population size were related to environmental features, which in turn are known to be driven by the time since deglaciation, and how (c) population sex-ratio changed in relation to time since deglaciation, and thus across space.

2. Materials and methods

2.1. Study area, and study system

The focus area was the foreland of Vedretta d'Amola glacier (Central-eastern Italian Alps; 46°13′16″–10°40′41″) (Fig. 1), which is a debris-covered glacier of 82.1 hectares (summer 2012), two/thirds covered by stony debris with variable depth, from a few centimeters to about one meter. The glacier foreland is 1.23 km long, covers an altitudinal range of about 150 meters, and is characterised by a moraine system dating back to the Little Ice Age "LIA" (c. AD 1850). Several sources (e.g. maps, reports, and records of length change) allowed the reconstruction of the glacier tongue position during the Little Ice Age, in 1925, in 1994, and in 2003 (Fig. 1). Annual mean soil temperature, recorded during the period 15 July 2011–14 July 2012, was 3.1 °C, while mean relative air humidity was 94.3% (datalogger located at about 15 cm depth in the stony debris at site 10, see Fig. 1). Annual mean temperature in the supraglacial debris was 0.5 °C (datalogger located at 10 cm depth at site 2, see Fig. 1).

On the supraglacial debris (mean elevation: 2642 m) the total plant cover is <10%; along the glacier foreland (mean elevation: 2520 m) the plant cover ranges from 5% to 70% and outside the glacier foreland (mean elevation: 2426 m), the total plant cover is >80%.

2.2. Study organisms

We studied three carabid beetle (Coleoptera: Carabidae) species: *Nebria germari* Heer 1837, *Oreonebria castanea* (Bonelli 1810) and *Oreonebria angustata* (Dejean & Boisduval 1830). They are cold-adapted species (Gereben, 1995; Gereben-Krenn et al., 2011), restricted to alpine habitats (above 2000 m asl) and exhibit fragmented distributional patterns suggesting refugial occurrence (Kavanaugh, 1979). They are classified as "autumn breeders" (Brandmayr and Zetto Brandmayr, 1988), short-winged (brachypterous, thus with low dispersal ability) and they have nocturnal forage behaviour (mainly predating springtails) (Homburg et al., 2014). Note that the "autumn breeders" definition at high elevation implies summer (i.e. snow-free period) reproduction, oviposition in late summer, autumn and winter development of larvae, and emergence of adults (and thus recruitment into the sampled population) after snow melt and thus before the beginning of sampling activity (see following paragraph).

2.3. Sampling design

Eleven sampling areas were selected along a linear transect starting on the glacier surface and running 1.7 km onto the late glacial substrata outside the LIA moraines (Fig. 1). Areas indicated as "2", "4", "5", "8" and "10" were sampled in year 2011, whereas areas "1", "3", "6", "7", "9" and "11" were studied in 2012. Each area was classified to represent its state of deglaciation: Class 0 (not yet deglaciated–glacier surface; areas 4, 3, 2, 1), Class 1 (areas left by the glacier in 1994–2003; areas 6, 5), Class 2 (1925–1994; areas 8, 7), Class 3 (1850–1925; areas 10, 9), and Class 4 (Late Glacial Substrata ca. 10'500 yrs ago; area 11).

The three species were sampled by means of pitfall traps (Eymann et al., 2010), a quantitative collecting method whose catches are a function of species' true population size and activity (activity-density) (Greenslade, 1964; Thomas et al., 1998). In each sampling area we placed three traps located at least 10 m apart to allow for sample independence (Kotze et al., 2011), which led to a total of 33 pitfall traps positioned in the entire study area. Traps consisted of plastic vessels (7 cm diameter and 10 cm height) baited with a mixture of wine vinegar and salt. The traps were active