A century of chasing the ice: delayed colonisation of ice-free sites by ground beetles along glacier forelands in the Alps

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Running title: Time lagged spread in Carabids after glacier retreat

1　**Summary**

2　Climate change is affecting species distribution, composition of biological communities, and

3　species traits. Despite the growing body of knowledge on the reaction of species to climate change,

4　the potentially delayed response of species is still severely understudied.

5　In this paper we modelled the time needed by ground-living invertebrates to effectively react to

6　habitat modification induced by climate change in relation to dispersal abilities. We analyzed the

7　occurrence pattern of alpine ground beetles (carabids) along areas recently freed by retreating

8　glaciers in the Central-eastern Italian Alps, to test how the synergic effects of time since

9　deglaciation and environmental factors may affect the colonisation process.

10　Different times of response to climate change in ground beetles were found. Sites already hosting

11　the land cover type suitable for our study taxon, but ice-free for less than 100 years, are mainly

12　colonised by winged carabid beetles (which have high dispersal abilities and are mostly habitat

13　generalists). No, or very few, wingless species (slow colonizers and ecologically specialized) occur

14　within those sites. The overall pattern suggests that within a site, suitable land cover is established

15　prior to colonization, due to a strong joint effect of time since deglaciation and land cover type.

16　Long-lasting habitat development at the fine scale is likely to result in a lack of specific resources

17　(e.g. food items, or microhabitat), which is likely to contribute to delayed colonisation, which

18　potentially could be tied also to dispersal abilities. Whatever the reason, the existence of a time-lag

19　often equal to or greater than 100 years in species colonisation implies caution in predicting

20　species' occurrence shifts following climate change.

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22　**Key words:** Alps - carabid beetles - glacier forelands - MARS - time-lag.

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Predicting the response of species to climate changes has been one of the main challenges in recent decades for ecologists and conservationists. The responses of biocoenoses to climate changes are well documented in many published studies, and is demonstrated by latitudinal and altitudinal shifts in species distributions, alteration in physiology, reproductive biology, phenology, fitness and population dynamics of many taxa (McCarty 2001, Walther et al. 2002, Parmesan 2006). The main current challenge is to evaluate the time of the response to global change, as the rapid rate of the current climate change is a primary concern for wild species and ecosystem conservation.

Meta-analyses performed at wide geographical scales suggest quite rapid responses of several species to a warmer climate (Parmesan and Yohe 2003, Le Roux and McGeoch 2008, Loarie et al. 2009, Chen et al. 2011), but the possibility that many animal taxa may require a fairly long time to effectively react to climate changes has been poorly considered until now. The species that apparently do not display reactions to climate change may just have longer times of reaction, which could increase the time of colonisation and the risk of local extinction.

Despite being poorly investigated because of practical and experimental constraints, the time of response to climate change is essential to calibrate projections of range shifts caused by global change. Discrepancies between fundamental and realised niches are well known (Soberón and Peterson 2005, Soberón and Nakamura 2009), and scenopoetic, bionomic and dispersal factors all contribute to the resulting distribution (Soberón 2007, 2010). Current estimates of range shifts, mostly based on (Grinnellian) fundamental niches, i.e. the niche defined by scenopoetic variables (Soberón 2010), generally assume that a habitat is occupied by a species as soon as it becomes "suitable" for the target organism in terms of physical and structural factors (the scenopoetic ones, e.g. temperature, topography, land cover), but other factors could prevent species settlement, definitively or for a certain time (Pearson and Dawson 2003, Soberón and Peterson 2005, Engler et al. 2009, Lavergne et al. 2010): dispersal ability, barriers, interspecific interactions, lack of suitable micro-habitats, scarcity of food resources or other environmental traits may act against colonization (Soberón and Nakamura 2009, Soberón 2010), thus also increasing extinction risk. Therefore,

current approaches to estimate altitudinal range shifts, essentially based on species distribution

modelling, could lead to an overestimation of future colonisation and to a concurrent

underestimation of, for example, extinction rates.

Retreating glaciers are considered a clear abiotic indicator of climate change. The possibility

of reconstructing past glacier dynamics by dating the frontal moraines left by the glaciers during the

Holocene climate fluctuations, offers an extraordinary chance to investigate the effect of climate

change on living species (Walker et al. 2010). Terrains freed by retreating glaciers (glacier

forelands), with a well-known chronology of glacial recession, represent a relatively artefact-free

system for the detailed study on the time of response shown by species and communities (Matthews

1992, Bardgett et al. 2005). Studying colonisation dynamics (primary successions) along glacier

forelands provides a context with a spatial and temporal scale for understanding the nature of the

relationships between animals, vegetation, and the abiotic components (Ettema and Wardle 2002).

This kind of habitat is associated with great environmental changes, and species assemblages living

there are thus forced to adapt to those changes. Different times of reactions have been hypothesized

at the local scale for communities of invertebrates colonising ice freed terrains at high altitude in the

Alps, and specifically the areas of Holocene glacier retreat (Kaufmann 2002).

Knowledge of the time since deglaciation allows researchers to assess if habitats are

occupied by target species as soon as they become available, or whether more time is needed before

species can successfully settle on deglaciated areas. Studies on colonisation of recently deglaciated

areas are already available for plants (Grabherr et al. 1994, Caccianiga and Andreis 2004,

Caccianiga et al. 2006) and invertebrates (Hodkinson et al. 1998, Kaufmann 2001, Kaufmann 2002,

Hodkinson et al. 2004, Gobbi et al. 2006a, Gobbi et al. 2006b). As a general pattern, newly exposed

land surface such as glacier forelands are firstly and actively colonised by heterotrophic organisms

(Hodkinson et al. 2002), supported by allochthonous income of food provided by upward winds

(Coulson et al. 2003). Other species are likely to settle later (Kaufmann 2001), but knowledge on

75 the time of response and colonisation is still vague, despite the already mentioned importance of

76 such a time-lag between habitat availability and colonisation.

77   Recent evidence from high-mountain plants suggests that dispersal abilities may affect the

78 time of reaction to habitat changes (Dullinger et al. 2012), whereas comparable evidence for high-

79 mountain animals is still lacking. The aim of our paper is to investigate and describe the potential

80 occurrence of different times of response to habitat modifications induced by climate change among

81 carabid species, an invertebrate group which represent a good biological model for such a study,

82 thanks to the inclusion of species with different dispersal ability and habitat specialization.

83   Our work is virtually the first attempt to evaluate differences in the response time of species

84 to climate change at a fine spatial scale, and to analyse response time to environmental variation in

85 relation to different wing morphology, which is a crude descriptor of both dispersal abilities and

86 ecological specialization. Dispersal propensity or ability and habitat specialization have been

87 reported to affect pattern of occurrence and time of response to climate and habitat change in

88 butterflies (Warren et al. 2001, Simmons and Thomas 2004, Menéndez et al. 2006). Here, we

89 investigated whether ground-living specialized invertebrates (i.e. carabid beetles) are randomly

90 distributed among recently ice-freed sites, or their occurrence is affected by properties of ice-freed

91 sites and species traits (e.g. dispersal ability, ecological specialization). We tested whether such

92 differences in time of response to climate and habitat changes, reported for butterflies at quite large

93 scales, can be found also at a fine spatial scale in glacier forelands, where small spatial distances are

94 associated to large variation in time since deglaciation, and hence in the time available for habitats

95 to establish and to species to colonise.

96

Methods

Study system

Ground beetles (Coleoptera: Carabidae) colonising the bottom of the glacier forelands are used as a study model. We chose carabid beetles because they represent, along with spiders, the earliest stages of arthropod colonization in recently deglaciated alpine areas (Gobbi et al. 2007). Additionally, carabids represent an ideal biological model because they include morphological traits such as wing development (winged and wingless species), which give information about dispersal abilities (Brandmayr et al. 2005). Even if a clear expression of dispersal ability in carabid beetles is highly complex, being governed by many different environmental variables and life-cycle factors (Kotze et al. 2011), wing morphology can be considered a good surrogate of flight capability, and thus of dispersal ability/propensity (Lovei and Sunderland 1996). Winged species are good, early and fast colonisers (Kotze and O'Hara 2003), whereas wingless species are late colonizers that take longer to colonise a suitable site, and that show high frequency in habitats of the late successional stages (Brandmayr 1991, Gobbi et al. 2007). Winged colonisers generally show wide geographical range, generalist strategies, and tolerance of a wide range of ecological factors (Pizzolotto 2008). On the other hand, wingless species, which are slow colonisers, being *per pedes* colonisers (Brandmayr 1991), increase with increasing habitat persistency and time since the first colonisation (Lovei and Sunderland 1996). In addition, many studies have reported significant correlations between the proportion of winged/wingless species and the habitat maturity (serial stages) (Brandmayr et al. 2003, New 2010). On the basis of these distinctive features, carabids represent an ideal tool to investigate the existence of time-lag related to dispersal propensity and habitat specialization in response to modifications induced by climate change.

Considering that some carabid populations experience a dimorphic wing status (both winged populations as well as wingless populations), wing morphology was checked using a stereomicroscope in all the sampled species (and specimens) according to the following criteria:

123 winged species are those with wings longer than the elitrae, whereas wingless species are those with

124 wings shorter that the elitrae; therefore, dispersal ability is a function of carabid wing form (Lovei

125 and Sunderland 1996, Gobbi and Fontaneto 2008, Pizzolotto 2008). Specimens did not show wing

126 dimorphism in our study sample.

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129 **Study area**

130 Our work took place in the Central-eastern Italian Alps, where we investigated carabid beetle

131 assemblages at two neighbouring different sites: Forni glacier foreland (length: 2.5 km) and Cedec

132 glacier foreland (length: 0.5 km), both located on the western slope of Mount Cevedale (3757m

133 a.s.l.) (Fig. 1).

134   Forni glacier foreland (46°25' N, 10°34' E, average elevation of 2400 m, range 2150 –

135 2650; chronosequence oriented in a NE-SW direction) is characterized by a well-preserved moraine

136 chronosequence representing 155 years of Holocene glacier fluctuations stretching over a length of

137 about 2.5 km. Four main moraines are clearly visible in the bottom of the valley, and they were

138 dated as follow: 1850, 1904, 1926 and 1980. Detailed information on the vegetation types in the

139 bottom and the side of the valley is reported in (Gobbi et al. 2006b). In general in the area of

140 Holocene glacier retreat the pioneer community is dominated by scattered *Picea abies*, *Larix*

141 *decidua* and *Salix* spp., replaced above c. 2400 m a.s.l. by *Oxyrientum digynae*, and *Saxifrago*

142 *bryoidis-Poetum alpinae*.

143   Cedec glacier foreland (46°27' N, 10°35' E, average elevation of 2650 m, range 2600 –

144 2700; chronosequence oriented in a W-E direction) is characterized by three main moraines

145 deposited during the Holocene, and dated as follow: 1850, 1965 and 1986. Cedec foreland is shorter

146 than the Forni one, with a maximum length of about 500 metres. Detailed information on the

147 vegetation types in the bottom and the side of the valley is reported in (Gobbi et al. 2010). In

148 general the glacier foreland is dominated by *Caricetum curvulae* prairie in the Tardiglacial sites,

149 and by *Oxyrientum digynae*, and *Saxifrago bryoidis-Poetum alpinae* in the area of Holocene glacier

150 retreat.

151   Along the slopes of the valleys the vegetation and invertebrate communities are not

152 comparable with those colonising the glacier forelands, because on the slopes the biotic

153 communities are influenced by cryoclastic processes and by human activity (livestock grazing).

154 Besides, in the Forni foreland, some sites located on the sides of the glacier have been deglaciated

155 for a long time, and are close to sites recently freed from ice. Thus, we assume that all species are

156 potentially able to colonise all sites in the two glacier forelands, because of the reduced distances

157 between and among sites that have been free from ice for a long time and other sites (see Fig. 1).

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161 **Sampling protocol**

162 A total of 13 sampling sites were placed at the Forni glacier foreland, and five at Cedec one. In each

163 site sampling was done by using six pitfall traps located along a linear transect perpendicular to the

164 glacier foreland, each trap 10 m apart, and baited with a mixture of wine vinegar and salt (non-toxic

165 for the vertebrate fauna, e.g. marmot; Brandmayr et al. 2005). Thus a total of 78 traps were used in

166 the Forni glacier foreland, and 30 traps in the Cedec glacier foreland. The traps were reset every 20

167 days during the snow-free period (July-September). The sampling sites were positioned along a

168 transect covering the entire proglacial areas, from the glacier terminus to the areas untouched by

169 Holocene glacier advances (Late Glacial substrata). The transect included terrain adjacent the

170 glacial front, recent and stabilized moraines, and Late Glacial substrata. Each point corresponded

171 with a known substratum age. Data were collected during the years 2004 and 2005 in the Forni

172 valley, and 2007 in the Cedec Valley (Gobbi et al. 2007, Gobbi et al. 2010).

173   It has been possible to associate an age of deglaciation to each new sampling site using

174 various sources of evidence including reports, photographs, dated historical drawings, and records

175   of glacial retreat made over the last 100 years. The sites located on the substrata freed by the glacier

176   during the Late Glacial Maximum period have been defined as deglaciated since 10,000 years ago.

177   We considered at each sampling site the presence/absence of all species as a dichotomous variable

178   (0/1).

179

180   **Habitat variables**

181   For each sampling site, we recorded elevation (meters above sea level), slope (degrees), aspect (i.e.

182   the direction in which a slope faces; calculated as absolute number of degrees from South), land

183   cover (categorical: four types: alpine grassland, sparse vegetation, bare rock, glacier or permanent

184   snow; data derived from DUSAF 2.0, ERSAF & Regione Lombardia, fine-scaled land cover map

185   dating to 2006) and time since deglaciation (years; variable entered in the analysis after log-

186   transformation). The first four variables were calculated in a GIS environment, whereas the latter by

187   photographs, iconography, and records of glacial retreat made over the last 100 years.

188

189   **Statistical analyses**

190   Moran's I was used to test for spatial autocorrelation in environmental variables and in species

191   occurrence. All variables were not spatially autocorrelated (Moran's I test, all $p > 0.6$), except for

192   elevation (Moran's I test, $p < 0.001$), and there were no differences in number of species, average

193   slope and time since deglaciation between the two areas (all $p > 0.3$), thus we pooled together the

194   data from the two study areas.

195   To model the effect of habitat variables on species occurrence we used the multivariate

196   adaptive regression splines (MARS), a rather recent machine-learning technique (Friedman 1991,

197   Hastie et al. 2001), which is now increasingly used in ecology (Leathwick et al. 2005, Mac Nally et

198   al. 2008, Heinanen and von Numers 2009) thanks to its flexibility and ability to model complex

199   relationships in species-habitat studies (Elith and Leathwick 2007). MARS fits non-linear functions

200   by fitting linear segments (or piecewise linear basis functions) to the data, breaking predictors at

201 knots, allowing slope of segments to vary between knots while keeping the full fitted function

202 without gaps, breaks or steps, thus connecting adjacent segments at knots.

203   MARS is the ideal approach to analyse our dataset because i) it is a non-parametric

204 regression method, ii) it can model non-linear relationships, which were expected in our study

205 system, iii) it allows multi-response models, which are particularly meaningful in our work because

206 we deal with scarcely represented species and low sample sizes and, most importantly, because we

207 are particularly interested in determining what factors are more likely to be important across all

208 species. Multi- species models have been shown to better perform than single-species models for

209 poorly represented taxa (Elith and Leathwick 2007).

210   We used the *earth* package version 3.2-1 (Milborrow 2011a) in R 2.14.0 (R Development

211 Core Team, 2011), which allows MARS analyses for different types of distribution, including

212 binomial distribution, which we used for multi-response models with presence/absence as

213 dependent variables (Milborrow 2011a; http://cran.r-project.org/web/packages/earth/index.html).

214 Model fitting was achieved by a forward procedure which identifies many potential predictors and

215 knots, on the basis of a specified increase in model performance (the "threshold" reported below),

216 followed by a backward pruning which reduced the number of predictors and knots on the basis of a

217 penalty value. We used the following settings for model selection: threshold = 0.001, penalty = 3,

218 degree of interactions = 2. The *plotmo* package version 1.3-1 (Milborrow 2011b) was used to plot

219 the fitted functions.

220   We modelled the potential effect of the five habitat variables described above and of their

221 interaction on the occurrence of carabid species, analyzed by means of a multi-response model. To

222 avoid potential biases due to the inclusion of very rare species, which could be accidentally

223 sampled, we re-ran the analyses after excluding the four species occurring with only one or two

224 individuals over the total sample; results were identical, so we presented only the all-species model.

225

Results

The spatial distribution and the dispersal ability of 22 species have been analyzed (Table 1). Moran's I test was non-significant for all species but one (*Oreonebria castanea*; $p < 0.001$).

The occurrence of carabid species according to the multi-response model was affected by the interaction between the land cover type 'sparse vegetation', and the time since deglaciation (Table 1). The multi-response model had fairly good explanatory power, with an overall R^2 equal to 0.30. On the basis of the coefficient indicating the effect of time since deglaciation given the land cover type, 15 out of 22 species were positively affected by time since deglaciation, four were negatively affected by it, and three were not or weakly affected (absolute value of the coefficient < 0.05). Out of 12 wingless species, one (*Oreonebria castanea*, the only species for which a significant spatial autocorrelation in occurrence pattern was found) was negatively affected by time since deglaciation, two were weakly affected, and nine were positively affected. Three out of 10 winged species were negatively affected by time since deglaciation, one was weakly affected, and six were positively affected.

For eight out of 15 species positively affected by time since deglaciation, modelled relationships suggested that the time since deglaciation has no effect until a cut-off point (varying from one species to another, but around 100 years for most of taxa), after which the positive effect of time since deglaciation becomes extremely strong (Figs. 2 and 3). In detail, for all but one of the wingless species positively affected by time since deglaciation, such positive effect became important after c. 100 years (Fig. 3), the only exception being *Carabus depressus*, for which the effect of time since deglaciation was roughly linear. On the other hand, none of the winged species (with only the partial exception of *Nebria rufescens*) displayed this kind of delayed response to time since deglaciation (Figs. 2 and 3).

Discussion

Our work is one of the few attempts to simultaneously model the effects of topography, land-cover, and time since deglaciation on the occurrence probability of animal species inhabiting glacier forelands. We investigated what environmental factors are likely to be more important in the occurrence of all carabid species in our study system, by means of a multiresponse model. Elevation had no effect on species occurrence (confirming previous assumptions often made in studies on glacier forelands), whereas the land cover type 'sparse vegetation' was important (in interaction with the time since deglaciation) in determining species occurrence and number, despite being just a macroscopic characterization of the vegetation. This finding outlines the importance of macroscopic habitat structure, in addition to microclimate and microhabitat (Gillingham et al. 2012). The positive effect of 'sparse vegetation' is in accordance with the higher number of species at sites placed at intermediate steps along the successional stages (mid-successional stages) (Kaufmann and Raffl 2002).

The key finding of our work is the occurrence of a time lag between the habitat changes induced by climate change and the reaction displayed by carabid species: a delayed response to environmental modifications due to glacier retreat was found in several species, and was strongest in non-flying carabids (the slowest colonizers, also with more specialized habitat requirements). We found a strong and widespread effect of time since deglaciation (in interaction with the land cover type) on the responses to habitat modifications caused by climate change displayed by high altitude carabids. For all but one wingless species, we found a positive effect of the time since deglaciation, which became important for the majority of species only after c. 100 years. The exceptions to this pattern were *Carabus sylvestris* and *C. depressus*, for which the effect was mainly linear, *Notiophilus aquaticus*, for which the effect was negligible, and *Oreonebria castanea*, which was slightly negatively affected by time since deglaciation, being a rather widespread species living also on the glaciers itself, and showing morphological adaptive capacity in relation to changing microclimatic conditions triggered by time since deglaciation (Gobbi et al., 2010). The two *Carabus*

276 species are generalist species occurring across different habitats, and were found in several sites.

277 *Notiophilus aquaticus* is probably limited by humidity, as it is a hygrophilic species tied to cooler

278 soils (Brandmayr and Brandmayr 1988), and was found only in four sites. The occurrence of such a

279 time lag is consistent with the prediction that less mobile taxa have steeper gradients over time and

280 space in colonisation probability than more mobile taxa (Baselga et al. 2012), and with the different

281 type and time of reactions reported for taxa with different degrees of dispersal ability and habitat

282 specialization (Menéndez et al. 2006).

283 The time lag between the achievement of environmental suitability at a given site in terms of

284 land cover type and climate patterns, and the actual occupation by a living species, is a potentially

285 critical point for the interpretation of projected shifts in species distribution in response to climate

286 change. Such a time lag may be determined by lack of essential resources, such as microhabitats or

287 specific food items, as well as by slow range expansion. Whatever the reason, the time lag in

288 response to environmental changes triggered by climate change has important implications for our

289 understanding and prediction of biodiversity loss, and of shifts in range and distribution in living

290 species and biological communities.

291 Our results highlight different time of response to glacier retreat triggered by climate

292 change, and a potential association between time since deglaciation and dispersal

293 abilities/ecological specialization: wing morphology is a proxy for species' dispersal propensity and

294 ecological specialization, and wingless species, which have limited dispersal and high ecological

295 specialization, display the strongest delay in the response to habitat modifications. These findings

296 are consistent with previous ones (Kaufmann 2001, Gobbi et al. 2006b), but give new insights into

297 time-effects affecting species occurrence, confirming how biological communities may require

298 decades or centuries to adapt to climate change, because of 'colonization lags' (Menéndez et al.

299 2006), even at such a small spatial scale as the one we investigated. This time lag has important

300 implications for modelling the ecological niche and its variation in time, and further emphasizes

301 how scenopoetic factors may still be important within hundreds or even tens of metres (Hortal et al.

302   2010). At this 'local' scale, much detailed information on factors potentially shaping the species-

303   habitat association is available, but could be insufficient, as soil development and other micro-

304   habitat features are often hardly quantifiable. For many species, time since deglaciation could

305   potentially represent a good proxy for micro-habitat development.

306   The significant effects of the interaction between land cover and time since deglaciation

307   clearly suggest that carabid occurrence is driven by a combined effect of the two environmental

308   factors. Sites already hosting the preferred land cover type, but freed from ice for less than 100

309   years, are colonized by no, or very few, wingless species. Wingless species are slow colonizers

310   because they are only able to colonize new areas by walking, and/or because they are, according to

311   different authors (Pizzolotto 2008, Gobbi et al. 2010), ecologically specialized (e.g. long larval

312   development, selective diet both at larval and adult stage). The overall pattern suggests that suitable

313   land cover is reached in a given site, and then species gradually colonize sites according to time

314   since deglaciation. Given the lack of sufficient information on effective dispersal and ecological

315   specialization (wing morpohology is a proxy for both), it is impossible to disentangle the relative

316   importance of slow speed of colonization and of micro-habitat specialization, respectively, on the

317   existence of such a time-lag. Some observations suggest that dispersal ability and ecological

318   specialization could jointly affect the time of colonization. Sites with very different ages of glacier

319   retreat and identical land cover are often close to each other in our study areas (Fig. 1). A general

320   lack of spatial autocorrelation in distribution pattern was detected, and the wingless species not

321   displaying the 100 yr lag were either the ones known to be habitat generalist, or those tied to

322   habitats not affected by time since deglaciation. Together, these observations suggest that habitat in

323   the first period after land cover consolidation may lack specific resources (Gobbi et al. 2010), such

324   as the availability of suitable food items, or unsuitable micro-habitat structure, and that the time

325   required to the development of suitable condition is around 100 years for many species. On the

326   other hand, time since deglaciation and time-lag are much more important for wingless species than

327   for winged ones, this finding alone suggesting a potentially non marginal effect of dispersal ability

328   on time of colonisation.

329   Coherently with the colonisation patterns of the spiders along the glacier forelands (Gobbi et

330   al. 2006b), carabid beetles also experienced the existence of a time-lag often around 100 years in

331   species colonisation. This time lag, displayed by these two different taxa, and along two different

332   glacier forelands, implies caution in predicting species' range shifts following climate change. On

333   the other hand, the occurrence of such a time-lag contributes to the debate about the potential

334   positive correlation between slow colonization and the extinction risk (Warren et al. 2001,

335   Menéndez et al. 2006). Dispersal ability is likely to be important in determining future distribution,

336   especially in the case of species experiencing an increase in habitat availability due to climate

337   change (Engler et al. 2009), as could be the case of invertebrate species colonising high altitude

338   areas. According to Kotze and O'Hara (2003), during the last century slow colonisers declined in

339   the European lowlands. Similarly, our results suggest that delayed colonisation of wingless species

340   could have a strong effect on the future pattern of species distribution/extinction in the Alps,

341   specifically near pro- and peri-glacial areas.

342

343   **Conclusions**

344   Current procedures to assess species range shifts due to environmental changes are typically based

345   on the identification of a species' response to the environment in the present context, mostly on the

346   basis of bioclimatic, topographic and land-cover variables, and on projection of its future

347   distribution by definition of the spatial extent of areas compatible with the measured environmental

348   response under projected changes. This approach is complicated by many factors, including

349   demography, spatial scale, adaptive potential and inter-specific relationships (Lavergne et al. 2010,

350   Heino 2012, Filz et al. 2013). Methods for dealing with distributional disequilibrium have been

351   developed (see e.g. Heikkinen et al. 1994, De Marco et al. 2008), and dispersal has been also

352   considered in predicting distributional shift (Coetzee et al. 2009, Engler et al. 2009), but several

studies focussing on altitudinal range shifts in alpine environments and covering large numbers of species are currently based exclusively on species distribution models. Our findings suggest that such an approach could lead to an underestimation of, for example, extinction rates, due to an overestimation of colonisation of new sites. Faster warming (as proposed by IPCC 2007) in the near future could be very problematic for many species. The delayed colonization of apparently suitable habitats due to a time-lag in response to changes is thus a further element of caution required in modelling response to changes driven by climate warming. This time-lag can be difficult to evaluate for several species or communities, and we are aware that our model system provided by glacier forelands could be particularly suitable for these kinds of assessments. However, care should be used when projecting occupation of newly available environments, especially by habitat specialist taxa and specialized communities (which are often of priority importance for conservation) in mountain, alpine and sub-arctic areas, where the development of suitable micro-habitats on soils previously covered by ice or snow can require much more time than the transition to a new type of land cover.

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Table 1 Full list of sampled species, abbreviated names (acronyms), wing morphology ("wing m.";
W = winged; L = wingless), ("N° sites"; the total number of sites surveyed is equal to 18 for all
species), coefficients of the multi-response model for occurrence of carabid species, which was
affected by the interaction between the land cover type of sparse vegetation and the time since
deglaciation. "B" represent the coefficient of the interaction term land cover sparse vegetation * log
of time since deglaciation. Positive values represent a positive effect of time since deglaciation on
probability of species occurrence, whereas negative values indicate a negative effect of time of
glacier retreat on probability of species occurrence. '100 yr lag' indicates the occurrence of a time-
lag around 100 years in the modelled effect of time since deglaciation on species occurrence (see
text).

Figure 1. Location of the study areas: the two glacier forelands are shown as black polygons in the
north-eastern corner of Lombardy. Approximate location of Lombardy within Italy is also shown.
The white dots represent to the sampling sites (northern group: Cedec; southern group: Forni).
Detailed maps show land cover type (open circles: alpine grassland; black circles: glacier or
permanent snow; black triangles: bare rock; black squares: sparse vegetation), time since
deglaciation (number of years reported along site location) and contour lines (100-m intervals; in
grey with elevation in m above sea level) for sample sites in Cedec glacier foreland (A) and Forni
glacier foreland (B). Area shaded in grey represents the current glacier position.

Figure 2. Modelled effect of the interaction between land-cover type (abbreviated 'landuse';
category 2: sparse vegetation; other categories: alpine grassland, bare rock, glacier or permanent
snow) and time since deglaciation (log-transformed; abbreviated 'deg_log') on the probability of
occurrence of winged carabid species. For abbreviation of species name (at the top left of each
specific plot) see Table 1.

Figure 3. Modelled effect of the interaction between land-cover type (abbreviated 'landuse'; category 2: sparse vegetation; other categories: alpine grassland, bare rock, glacier or permanent snow) and time since deglaciation (log-transformed years since deglaciation; abbreviated 'deg_log') on the probability of occurrence of wingless carabid species. For abbreviation of species name (at the top left of each specific plot) see Table 1.