

NEWS AND VIEWS

PERSPECTIVE

A re-appraisal of nunatak survival in arctic-alpine phylogeography

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A long standing and at times fervid debate in biogeography revolves around the question whether arctic and high alpine organisms survived Pleistocene ice ages on small island-like areas protruding above the ice-sheet, so-called nunataks, or whether they did so in peripheral nonglaciated refugial areas. A common picture emerging from a plethora of molecular phylogeographic studies in the last decade is that both in the Arctic and in temperate mountain ranges such as the European Alps nunatak survival needs to be only rarely invoked to explain observed genetic patterns (for a rare example see Stehlik *et al.* 2002). As two studies in this issue show, depreciation of the nunatak hypothesis is, however, not warranted. In this issue of *Molecular Ecology* Westergaard *et al.* (2011) investigate genetic patterns of two arctic-alpine plant species distributed on both sides of the Atlantic exclusively in areas that were mostly covered by ice-sheets during Pleistocene glacial advances. In both species, amplified fragment length polymorphism (AFLP) data identified divergent and partly genetically diverse groups east and west of the Atlantic. This suggests, for the first time in Arctic plants, *in situ* survival on nunataks. In an entirely different geographic setting and on a different geographic scale, Lohse *et al.* (2011, this issue) study the colonization of high alpine areas in the Orobian Alps, situated within and adjacent to a prominent peripheral refugial area (massif de refuge) in the Southern Alps of northern Italy, by dispersal-limited carabid ground beetles. Using explicit hypothesis testing and inference of ancestral locations in a Bayesian framework, stepwise colonization from two separate southern refugia is found to shape the genetic pattern of these beetles, but at the northern edge, populations survived at least parts of the last glaciation *in situ* on nunataks.

Keywords: arctic, European Alps, nunatak, phylogeography, postglacial colonization, refugia

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It has long been understood that Pleistocene climatic fluctuations had tremendous impact on shaping the history of the fauna and flora on Earth. An obvious question for organisms occurring in areas covered by glacial ice-sheets, such as northern Europe or the European Alps, is where did they survive then? Most biogeographers from 'pre-molecular' times favoured *in situ* glacial survival on nunataks (Brockmann-Jerosch & Brockmann-Jerosch 1926; Holdhaus 1954; Hultén 1958), which in part was motivated by the presence of dispersal barriers, such as the Atlantic Ocean, that were considered insurmountable for arctic-alpine taxa. In the molecular era, however, it became increasingly clear that assumed dispersal barriers are leaky and that the vast majority of studied organisms re-colonized once glaciated areas postglacially from refugia outside the ice-sheets (Brochmann *et al.* 2003; Schönswetter *et al.* 2005; Alsos *et al.* 2007). In view of this, it was concluded already in the early days of arctic phylogeography that 'glacial survival does not matter' (Gabrielsen *et al.* 1997). Inferences from genetic patterns will, however, be misled in cases, where local survivors are genetically swamped by massive immigration from re-colonizing conspecific populations (Gabrielsen *et al.* 1997), leading to an underestimation of the relevance of nunatak survival. Species most probably to retain a molecular signature of *in situ* survival are therefore those which possess little potential for rapid range expansions and re-colonization, as deduced from, for instance, current distribution patterns or species ecology. This is the case for the organisms studied by Westergaard *et al.* (2011) and Lohse *et al.* (2011), and significantly, in both cases, convincing evidence for nunatak survival is found.

Westergaard *et al.* (2011) investigate *Arenaria humifusa* and *Sagina caespitosa* (Fig. 1), two species of the carnation family (Caryophyllaceae) with similar distributions on both sides of the Atlantic Ocean (from northeastern North America via Greenland to Scandinavia and Svalbard) and no occurrences in southern or central European mountain ranges. Species showing this distributional type have been grouped into a 'west-arctic element', and they have served as strong argument in favour of the nunatak survival hypothesis in northern Europe. The alternative hypothesis is that northern European populations are the result of postglacial colonization from North America (Nordal 1987). (A third alternative is survival in southern refugia, where the species later became extinct, but this hypothesis is less parsimonious and, therefore, not considered here.) The two hypotheses differ in the predicted patterns of genetic variation. Nunatak survival is expected to result in strong



Fig. 1 *Arenaria humifusa* and *Sagina caespitosa* (left and right insert, respectively) are rare, arctic-alpine pioneer species found scattered throughout their quite extensive 'west-arctic' distribution ranges. In the arctic archipelago of Svalbard (panorama from Kongsfjorden), *A. humifusa* has four stations, whereas *S. caespitosa* only has two (photo credits: KB Westergaard, IG Alsos, KI Flatberg).

genetic structure separating eastern populations from the others, whereas postglacial long-distance colonization would be manifested by high genetic similarity across the Atlantic Ocean and an eastward leading-edge pattern of decreasing genetic variation. The pattern observed in the amplified fragment length polymorphism (AFLP) data agrees well with the expectation from the nunatak survival hypothesis: in both species, eastern populations are genetically distinct from western ones, and each group has many exclusive markers indicative of isolation in separate refugia. *In situ* survival on nunataks does, however, not imply distributional stasis. This is evident in both species from postglacial contact zones in Greenland and Iceland as the result of trans-Atlantic dispersal, commonly observed in arctic-alpine species despite their lack of obvious long-distance adaptations (Schönswetter *et al.* 2008).

Lohse *et al.* (2011) study a species complex of the carabid beetle genus *Trechus*. This genus has a world-wide distribution with highest species diversity and rates of endemism in mountain ranges, including the European Alps. The authors focus on members of the *pertyi* group (Fig. 2), which has undergone a radiation in the Orobian Alps in northern Italy. Whereas the southern parts of the Orobian Alps constitute a well-known massif de refuge, the northern parts were situated within the continuous glacial ice-sheet with protruding peaks acting as nunataks (peripheral nunataks *sensu* Schönswetter *et al.* 2004). (It should be noted that the classical literature on nunatak survival in the Alps refers to nunataks in the central not the marginal parts of the Pleistocene ice-sheets). As *Trechus* beetles are wingless and are therefore expected to be slow dispersers, rapid re-colonization from potential refugial areas and genetic swamping of potential nunatak populations seems unlikely. Here, a pure nunatak survival model (each popu-



Fig. 2 *Trechus* beetles (shown here *T. brembanus*) in the Orobian Alps are found around alpine lakes, such as Lago Rotondo (photo credits: D Obbard, M Müller).

lation descends from a glacial *in situ* population) is contrasted with an extreme founder event model (each population is founded by just a single lineage without further gene flow between populations). These models differ in the predicted gene genealogies and population coalescent times. Pure nunatak survival is expected to result in monophyletic population clades (likely small population sizes in *Trechus* beetles reduce the chance of lineage sorting), whose coalescence times predate the postglacial, whereas successive founder events would lead to a nested series of paraphyletic population groups with coalescence times depending on the times of the founder events. Based on mitochondrial sequence data, a mixture of both models is found in *Trechus*. Stepwise colonization involving sequential founder events, likely starting from refugial populations in the southwest and the southeast of the Orobian Alps, is supported by both Bayesian topological constraints testing as well as by a novel method of Bayesian ancestral location testing (Lemey *et al.* 2009), the most likely founder of most populations being directly adjacent populations. On the other hand, several populations from the northern ridge are monophyletic and have coalescence times older than the onset of the postglacial, suggesting *in situ* survival at least during part of the last ice age.

The importance of the studies of Westergaard *et al.* (2011) and Lohse *et al.* (2011) is twofold. For one, the hypothesis of nunatak survival is brought back into the phylogeographic arena, and the prevailing evidence for postglacial re-colonization appears to be at least in part a consequence of high colonizing capabilities of the investigated species. Second, nunatak and peripheral survival are not mutually exclusive and may both be involved in an organism's Pleistocene history, yet potentially acting at different time scales. As nicely shown here for Alpine beetles (Lohse *et al.* 2011), both hypotheses actually are mere end-points of a continuum (see also the concept of 'peripheral nunataks' by Schönswetter *et al.* 2004) and a near-ideological either-or discussion is as dispensable as that over the

explanatory superiority/inferiority of vicariance versus dispersal in historical biogeography. Instead, the introduction of high-throughput sequence generation (Emerson *et al.* 2010) and of increasingly sophisticated data analyses to phylogeography (Lemey *et al.* 2010) as well as the reconstruction of past vegetation via DNA barcoding utilizing ancient DNA conserved under permafrost conditions (Sønstebø *et al.* 2010) open exciting new possibilities for studying the dynamics of Pleistocene range shifts.

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