

## **Refugial capacity defines holdouts, microrefugia and stepping-stones**

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### **Introduction**

Refugia are habitats that populations can retreat to as prevailing climates become inhospitable, and potentially expand from should climates again become favourable [1]. They therefore potentially facilitate the long-term persistence of populations, despite changes in the regional climate. The importance of refugia for the survival of populations under anthropogenic climate change is increasingly recognised [1,2]. As a result, they are now considered keys to conservation planning under climate change [3,4].

Hannah *et al.* [5] recognise microrefugia —refugia of small geographic extent (after 6,7) — and distinguish between holdouts, microrefugia and stepping-stones. Microrefugia are considered places of unusual microclimate in which populations persist, while holdouts enable persistence for a limited time under deteriorating climates. Stepping-stones occupy microclimates successively to facilitate range shifts. Because refugia have limits to

facilitating persistence, Hannah *et al.* [5, pg. 390] state that “conservation strategies need to be built around holdouts and stepping-stones, rather than low-probability microrefugia”.

We suggest that holdouts, microrefugia and stepping-stones should be considered different aspects of the continuum that defines refugia. We argue that, subdividing refugia in this way has merit for the retrospective analysis of population dynamics. However, the approach is of limited utility in conservation planning because of the unidirectional nature of anthropogenic climate change. We therefore suggest greater attention is required to quantify and manage around the more important component of refugia in conservation planning — their capacity as refugia [8].

### **Microclimatic stability versus population dynamics**

Species are adapted to particular suites of environmental conditions [9]. Should these conditions change, populations must migrate, adapt or locally fine-tune to suitable microhabitats [e.g. 10], if they are to avoid extinction. Populations undergo range shifts as a result of migration to track favourable climatic conditions [e.g. 11]. Holdouts and stepping-stones are important facilitators of such range shifts (Figure 1). However, refugia are based on unique, relatively stable microclimates that facilitate survival of populations regardless of the climatic suitability of their surrounds. Hence they buffer against predominant or regional climatic conditions. Indeed, different types of refugia can be identified based on the type of environmental conditions that they buffer [12].

### **The capacity of refugia**

While refugia facilitate the persistence of populations under adverse climatic conditions, they have limits in the level of buffering from prevailing conditions that they can provide. If climatic conditions continue to deteriorate, refugia eventually become unable to maintain

conditions that enable survival for that population. The level of buffering provided by this continuum is the capacity of the refugium [8].

Global climate projections are now unidirectional (e.g., Figure 2 in [5]). The separation of stepping-stone, holdout and microrefugia components [sensu 5] of the refugium continuum is therefore rendered impotent for conservation planning under anthropogenic climate change. All three proposed components are refugia, as they retain environmental conditions not available in the surrounding landscape. They therefore facilitate the persistence of populations when the surrounding landscape cannot (Figure 1). However, microrefugia have greater capacity as refugia than holdouts or stepping-stones.

The capacity of refugia is therefore a more useful concept for landscape level conservation planning under anthropogenic climate change than the separation of refugia into holdouts, microrefugia and stepping-stones. The latter designation can only be determined retrospectively, after populations have responded. Furthermore, refugial capacity facilitates prioritisation of potential refugia based on their ability to safeguard the survival of species under anthropogenic climate change. For example, quantifying the capacity of refugia allowed determining important refugia in Tasmania, Australia, to the year 2100 under different climate change models [8] and protection of almost 95% of the less frequently occurring plant taxa.

## **Conclusion**

Anthropogenic climate change is causing species to shift their distributional ranges. Presumably, along these journeys particular sites will serve as stepping-stones, holdouts and microrefugia — but the capacity of these refugia determines their effectiveness and the level of buffering provided. Determining refugial capacity allows prioritisation of sites as refugia in conservation planning and allows the protection of locations likely to provide the best

chance for populations under anthropogenic climate change. It is therefore more important to quantify the capacity of refugia than to conceptually subdivide them into microrefugia, holdouts and stepping-stones.

## References

(Max: 12 references)

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## **Figures**

Figure 1. Refugia (including holdouts, microrefugia and stepping-stones) for a hypothetical species in space and time in relation to changing environmental conditions. Grey shaded areas indicate the space occupied by the species through time and arrows dispersal events. Holdouts, microrefugia and stepping-stones interchange in time and space under anthropogenic climate change. Black dots indicate the location of refugia of varying capacity at different points in time and how these relate to the terminology proposed by Hannah *et al.* [5].

