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.

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Place and process in conservation planning for climate change: a reply to Keppel and Wardell-Johnson

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Conservation in the face of climate change is hindered by a preoccupation with place. 'Refugial capacity' [1] adds useful descriptive power to the terminology of place, while 'stepping stones' and 'holdouts' are terms that usefully describe the dynamics of place [2]. Ultimately, no matter what happens in the lexicon, conservation needs to be implemented with a shift in focus from place to process. It will not be easy.

Biological conservation targets are species and ecosystems that are constantly shifting with respect to place in response to climate and other global change factors. Yet, our most effective conservation tools are protected areas – places. It is thus understandable that planning for conservation and its associated terminology is deeply preoccupied with place. The growing recognition of the importance of process makes it difficult to reconcile the tradition of place with the need to put process at the center of conservation planning. This does not mean that protected areas are irrelevant. Place-based conservation is the single most effective tool in the conservation repertoire and will

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continue to be so. However, our planning focus needs to shift from place to process.

Cowling *et al*. defined pattern and process as separate elements in systematic conservation planning [3]. Pattern was the distribution of species across a landscape, resulting in unique assemblages at each place. Process included evolution and shifting geomorphology. Why do we see present pattern as static when we understand so well that patterns continually change – that in fact what we are studying is not a pattern, but a moment in dynamic process? It is likely to do with our preoccupation with place, our place-centric terminology and the inherent difficulty in grasping change that unfolds on timescales that are long relative to a human lifespan.

Now, human-induced climate change is speeding up the game, making it impossible to pretend that pattern and place are synonymous. It is clear that modern conservation planning needs a paradigm focused on process, not pattern.

Microrefugia are the last gasp of place-based conservation planning. We now know that microscale processes are important and that they have macroscale implications. However, if we think that means there are small places that do not change, we are surely mistaken – they simply change at different rates. We still must plan for process.

Precedents exist. In fire management, the historical range of variability (HRV) in fire characteristics (sizes, frequencies, intensities, and seasonalities), their complex effects, and landscape-scale vegetation composition has long been used in understanding the role of wildfire as a crucial natural disturbance in a given ecosystem [4–6]. Conservation in fire-prone environments may thus depend as much on wildfire as a process, incorporating factors that control ongoing fire regimes and avoiding critical thresholds [7], as on protecting a particular piece of landscape. Conservation planning for climate change needs an analogous paradigm. Understanding the relative importance of climate shifts and their conservation implications will hinge on an understanding of the processes in question.

Conservation planners have begun to embrace this challenge, developing conservation planning tools that explicitly address change. For example, conservation planning tools are available that explicitly incorporate simulated range movements of species with climate change [8,9]. Dynamic vegetation models, Earth System Models, physiological models and others focus on the dynamics of change, although not all have been fully integrated into conservation planning. Terms such as 'topographic buffering' are emerging, which emphasize process over place.

Conservation planning for climate change is not about place; it is about dynamics. However, these dynamics can lead us to places in which our traditional place-based conservation tool, protected areas, can make a difference in a dynamic world. Partial solutions that skip the dynamics by 'conserving the stage', banking on microrefugia that do not change or ignoring climate change altogether, will not be robust throughout the rest of this century. Conservation planning for climate change will be effective when dynamic planning tools are widely used and incorporate fine-grain effects, empowering conservationists to move from a paradigm focused on places to one focused on dynamics.

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How (not) to review papers on inclusive fitness

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Evolutionary fitness of traits or behaviors is inclusive [1] of their 'direct' effects on the trait bearers' reproduction and their 'indirect' effects on others' reproduction (Figure 1). Inclusive fitness models lay bare that traits can be selectively advantageous even when they negatively impact direct fitness. A capstone of this approach is that Darwin's dilemma of sterile workers and nonreproductive helpers seems neatly solved by the simplicity of Hamilton's Rule ($rb - c > 0$). Workers work and helpers help to maximize

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