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# Unequal contributions of species' persistence and migration on plant communities' response to climate warming throughout forests

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**Community reshuffling is lagging behind climate warming for many taxa, thereby generating a climatic debt. However, only few studies have attempted to assess the underlying factors that explain this debt. Here I examine how effects of species' migration and persistence on the current climatic debt vary spatially in forest herbaceous communities throughout the French territory. I show that Mediterranean communities are responding to climate warming through both high species' migration and persistence effects, while alpine forest is the only ecosystem where species' migration overtakes species' persistence mechanisms. Such an approach seems promising in assessing the underlying mechanisms of the biodiversity response to climate change locally, and it can be applied for conservation issues to assess biodiversity sensitivity and optimize its management.**

The concept of climatic debt or lag has been recently brought up to date in ecology (Menéndez et al. 2006) since its past development (Davis 1986). This debt assesses the time-delayed response of biological entities (e.g. species, communities or ecosystem) to climate change as a result of extinction debt and immigration credit (Jackson and Sax 2010). Studies have demonstrated that species composition in forest plant (Bertrand et al. 2011), butterfly, bird (Devictor et al. 2012) and freshwater fish (Comte and Grenouillet 2015) communities lagged behind the current climate warming. Factors involved in species' persistence and migration are expected to amplify and mitigate this lag by promoting the temporal inertia and reshuffling of species assemblages, respectively. Recently, it has been shown that factors involved in species' persistence absorb more of climate warming in communities than species' migration is able to mitigate through thermophilization of forest plant assemblages (Bertrand et al. 2016). The rare studies investigating the underlying factors that explain the climatic debt assumed this determinism was stable over large and heterogeneous areas (Bertrand et al. 2016, Gaüzère et al. 2017). However, it is likely to vary locally following the proportion of warm-adapted species present in the regional species pool as well as the magnitude of the climate change or the habitat connectivity and disturbances for instance (Bertrand et al. 2011, 2016).

Based on this conceptual framework, I examined the spatial nonstationarity of species' persistence and migration effects on the current climatic debt observed in French forest plant communities using geographically weighted regression (GWR; see Supplementary material Appendix 1 for a data and model description, and Supplementary material Appendix 2 for a discussion on the model validity and outputs). The factors involved in species' persistence accounted for in this analysis are tolerance to climatic stresses, temporal climatic niche shift (resulting from evolutionary adaptation, acclimation, and/or phenotypic plasticity), species longevity, soil quality, and microclimate buffering. Those involved in species' migration include climatic niche tracking, habitat connectivity, earliness of seed dispersal, and competition for water resources (contributing to select warm-adapted species in plant communities) (Essl et al. 2015, Bertrand et al. 2016). All these factors are directly informed or computed from 45 806 forest inventory observations used to fit the GWR model.

I show that the effects of species' migration and persistence highly vary throughout the French forest territory (Fig. 1A and B). The magnitude of both effects is greater in the southern than the northern part of France. The plant communities in Mediterranean forest are intensely responding to the

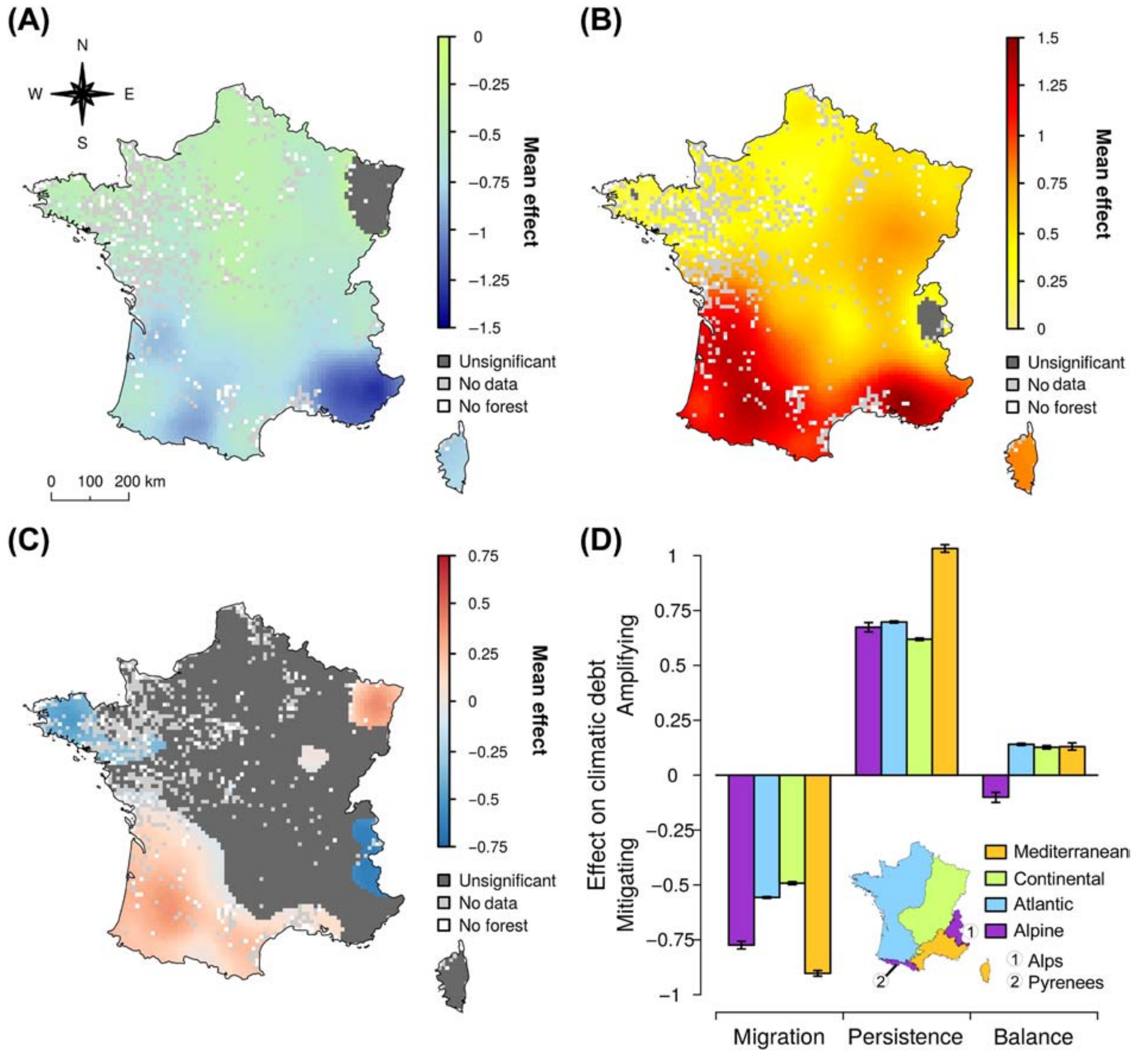


Figure 1. Spatial variation of the mean effects of migration (A) and persistence (B) mechanisms on the current climatic debt observed in plant communities throughout the French forests, and balance between both effects (C) (computed as the sum of mean effects of species' migration and persistence mechanisms mapped in panels (A) and (B), respectively). (D) Synthesis of species' migration and persistence effects in each French biogeographic region. Mean effects (and confidence intervals in panel (D)) are computed from 1000 bootstrapped models. More negative and positive values indicate higher mitigating and amplifying effects on the climatic debt, respectively.

current warming and display the highest effects of species' persistence and migration (Fig. 1A, B and D). This result likely corroborates the observed low sensitivity of these plant communities facing climate change (Vennetier and Ripert 2009) while other global change drivers can alter their sustainability (such as habitat loss and disturbance through fire and human actions; Sala et al. 2000). Mediterranean plants developed efficient adaptations to hot and dry conditions, which allow them to absorb part of the climate change and hence to persist in existing communities (Thuiller et al. 2005). By contrast, the high species' migration effect depicts a facilitated climatic niche tracking due to both rugged topography and proximity to Alps mountains that help species to find short-distance climatic escape leading to communities' thermophilization and high species turnover (Thuiller et al. 2005).

Furthermore, I show that alpine plant communities are the only communities of the four biogeographic regions observed in France with a species' migration effect taking over the species' persistence effect (Fig. 1C and D). Climatic niche is more easily tracked by species in highland than in lowland areas (median isotherm shift since 1960 = 35.6 and 1.1 km in lowland and highland areas, respectively, according to Bertrand et al. 2011), hence reducing the climatic debt (60.7% of temperature increase recovered in highland forests, according to Bertrand et al. 2011). However, such a pattern varies inside the alpine biogeographic region itself (Fig. 1C). The magnitude of the species' migration effect on the climatic debt is similar between Alps and Pyrenees mountains (–0.769 and –0.773 in average, respectively; Fig. 1B), but the effect of species' persistence is higher in Pyrenean forests (Fig. 1A) as their floristic assemblages are likely more efficient to tolerate hydric and thermal stresses (Supplementary material Appendix 2 Fig. A2).

In conclusion, I emphasize high spatial disparity in species' persistence and migration effects driving the forest plant community response to climate change. Reproducing such an analysis on other taxa should allow to get new insights on the nature, magnitude, and efficiency of mechanisms that biodiversity is implementing in the face of climate change. Predictive modeling will benefit these advances by preferentially integrating the most important drivers (Svenning and Sandel 2013). This approach is also promising for biodiversity conservation because it allows the assessment of how biodiversity is responding to environmental changes. Here Atlantic and Continental forest plant communities are likely more sensitive to the current warming due to both large climatic debt (Bertrand et al. 2016) and lower species' migration and persistence effects than Mediterranean and alpine communities (Fig. 1). Such kind of information will be useful in optimizing biodiversity management (e.g. through selecting best actions considering the mechanisms that drive the current biodiversity response to climate change) and in evaluating the efficiency of conservation actions (by assessing how they affect the biodiversity response to climate change).

Supplementary material (Appendix ECOG-03591 at <www.ecography.org/appendix/ecog-03591>). Appendix 1–2.

## Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.t351v0b> (Bertrand 2018).

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