Commentary

Isoscapes: a new dimension in community ecology

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The utility of stable isotopes in interpreting and recording aspects of environmental science, biogeochemistry, ecology and organismal physiology has long been established (Peterson and Fry 1987, Dawson et al. 2002). Examples range from the reconstruction of prehistoric human diets (Schoeninger et al. 1983) and tracing components of the hydrological cycle (Gat 1996), to differentiating C₃ and C₄ photosynthesis (Farquhar et al. 1989) and recording the humidity under which plants grow (Kahmen et al. 2011). Stable isotopes have proved invaluable in elucidating biological processes at multiple levels, and along with this there has been a recognition of the intrinsic information held within the observed patterns of stable isotopes across landscapes. For example, δ²H of stem water in understory plants has been used to define areas influenced by hydraulic lift (Dawson 1993), while patterns of δ¹⁵N have been used to calculate the contribution of marine-derived nitrogen to Sitka spruce growing near salmon-spawning streams (Helfield and Naiman 2001).

The term isoscape, first coined by Dr Jason B. West and Dr Gabriel J. Bowen (West et al. 2008, Bowen 2010), refers to any spatially explicit prediction of isotopic values across a landscape. They can be derived from interpolating geographically distributed observations or developed by process-level models that aim to capture and predict this observed heterogeneity from an understanding of isotope fractionation. In a comprehensive book, Isoscapes, edited by West et al. (2010a), a framework was established within which researchers may begin to understand movement, patterns and processes on Earth through the use of this isotope mapping.

The value of detailed spatial and temporal maps of isotopic composition is best exemplified in the field of hydrologic science. Initiated in 1958, operational by 1961 (Dansgaard 1964) and still continuing today, the International Atomic Energy Agency (IAEA) and World Meteorological Organization’s Global Network of Isotopes in Precipitation (GNIP) consists of 1000+ meteorological stations at which monthly precipitation is collected for δ¹⁸O and δ²H analysis. This spatially explicit data can subsequently be transformed into a continuous map depicting how moisture isotopes vary across the landscape (West et al. 2008, Terzer et al. 2013). This makes it possible to determine the probable isotopic signature for the water entering terrestrial systems at any point on Earth, providing numerous insights into environmental processes (Aggarwal et al. 2010). Moisture isoscapes have been used to inform our understanding of plant development processes (Kahmen et al. 2013) and by extension to resolve paleo-proxies (West et al. 2010b); they have (in conjunction with other elements) been used at large spatial scales to determine geographical origins of biological materials (Wunder 2010) and to track animal (including human) migration across the landscape (Hobson et al. 2010).

However, more recently, there has been a growing use of high-resolution isoscapes over limited spatial extents (i.e. field-scale studies) to answer more targeted ecological questions, such as the influence of micro-topography on nutrient cycling in pastures (Dixon et al. 2010) or the biophysical impacts of invading N₂-fixing exotic species upon native community structure (Rascher et al. 2012, Bai et al. 2013).

In this issue, Hellmann et al. (2016b) build upon previous work (Rascher et al. 2012, Hellmann et al. 2016a) by using isoscapes of δ¹⁵N and δ¹³C in leaf-tissue to resolve the spatial extent of plant–plant interactions between the invasive tree Acacia longifolia and three native plant species in a sand-dune ecosystem on the west coast of Portugal. Isoscapes were developed by pooling leaves of each native species found...
within 10 m² quadrats across two 1000 m² plots. Isotope ratios of these samples were then interpolated using ordinary kriging to produce continuous species-specific isoscapes. As an N₂-fixing legume, A. longifolia develops an isotopic signature in its organic matter more closely aligned with the δ¹⁵N of atmospheric N₂ (i.e. ~0‰). As this organic matter (~2‰) is deposited into the surrounding soil through root exudation, root mortality and leaf-litter fall the isotopic signature of inorganic nitrogen available for other plants to take up is made less negative (Figure 1). This leads to a characteristic change in the δ¹⁵N signature of non-fixing native flora. In using multiple isoscapes generated from the leaf isotopic composition of the native species, the authors are able to show that the ecological interactions within the community were (i) spatially explicit, (ii) species-specific and (iii) context dependant. For example, while two non-N₂-fixing species (Corema album, Pinus pinaster) showed the influence of the invader on nitrogen uptake between 5 and 8 m from the canopy edge of A. longifolia, the native N₂-fixing Stauracanthus spectabilis showed no apparent influence of Acacia upon its nitrogen cycling (Hellmann et al. 2016b).

As exemplified by Hellmann et al. (2016b), the interpretation and utilization of isoscapes at the 'field-scale' requires a detailed understanding of the studied ecosystem. It is only in the context of more traditional eco-physiological data examining the relative water use of native and exotic species (Rascher et al. 2011) and an appreciation of the potential for species-specific facilitation in growth rates (Hellmann et al. 2011) that single-pass isoscapes such as those conducted here can be properly interpreted. Similarly, the use of overlaid multi-elemental isoscapes have the potential to provide further insight into the nature of altered biochemical cycling. For example, within the studied dune ecosystem there is the possibility of coupling observed patterns in nitrogen and carbon isotopes with those of oxygen. Such an approach may make it possible to determine if adjustments in plant productivity and intrinsic water-use efficiency as suggested by δ¹³C are the result of the invading species altering water or nitrogen availability (Moreno-Gutierrez et al. 2012).

To date field-scale isoscapes often represent a single sampling event (or at least contain only limited temporal resolution). Nonetheless, the historical context and dynamic response of isoscapes to perturbations are clearly observed by Hellmann et al. (2016b) in the highly susceptible C. album. In this species, observed differences in the magnitude and extent of A. longifolia's impact upon its δ¹³C values is ascribed by the authors to the extent and coverage of the invading tree crown cover. It is clear that, as suggested by Strayer et al (2006), changes in the biophysical properties of an invaded landscape that result in an altered isoscape within native vegetation accumulate with time, and may persist long after the invasive species is removed (Marchante et al. 2009) (Figure 1).

Figure 1. Temporal progression of how an N₂-fixing exotic species may impact soil nitrogen and species-specific isoscapes in the leaves of two native species homogeneously distributed across a landscape. Situation (i) represents natural variation across an uninvaded landscape, (ii) the same landscape impacted by a single N₂-fixing tree and (iii) a complex landscape showing legacy effects after tree removal as well as the impact of further recruitment. The interpolated isoscape of native species 1 shows it to have a less negative δ¹⁵N value than species 2 at a given point in the landscape with no response to the exotic tree invasion. Species 2 in contrast shows a substantial change in its isoscape in response to a nitrogen cycle perturbed by the invasive tree. Studying the spatial and temporal dynamics of changing isoscapes can provide insight into the interactions between native and exotic species.
With the rapid expansion in the accessibility of high quality isotopic measurements, both with high-throughput isotope ratio mass spectrometry (IRMS) and the advent of isotope ratio infrared spectrometry (IRIS), researchers are now able to sample at an unprecedented spatio-temporal scale. When coupled to international projects to compile and standardize isotopic sampling efforts, such as IAEA’s GNIP and associated Global Network of Isotopes in Rivers (GNIR), it is clear that the use of large continental-scale isoscapes will become more routine. To that end there now exist global efforts to develop easily accessible, standardized tools for the spatial analysis of isotope data, such as IsoMAP (www.isomap.org) (Bowen et al. 2014). However, as demonstrated in Hellmann et al. (2016) there is also the possibility of ‘field-scale’ isoscapes being employed to answer directed questions concerning specific eco-physiological and community-level interactions. This use of field-scale isoscapes, while offering a powerful approach to advancing the application of stable isotope research to biological systems (Werner et al. 2012), will require the development of appropriate GIS techniques, a consideration of temporal context and a true integration with other lines of evidence. Hellmann et al. (2016b) have shown how such an application of sub-hectare isoscapes and the innovative application of spatial statistics can provide valuable insights into the community ecology of an important coastal ecosystem.

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References