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Global-scale coordinated networks as a tool for exploring the functioning of stream ecosystems

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ABSTRACT

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Individual ecological studies, although suitable for testing hypotheses and developing theory, provide site- or region-specific information that is difficult to extrapolate to provide broad generalizations. Today, emerging globally relevant questions (e.g., climate change, biodiversity loss, invasive species or habitat degradation) require a reconsideration of what approaches would be best for understanding large-scale ecological patterns and processes. A technique commonly used for this purpose is meta-analysis, a quantitative approach to reviewing, integrating, and summarizing large numbers of independent studies. However, the robustness of a meta-analysis relies on the individual studies selected for inclusion, and issues of scale and methodology cannot be controlled retrospectively. An emerging, alternative approach is global-scale coordinated experiments, run in parallel by several research groups in multiple locations around the globe. These experiments have the advantage of addressing global problems and exploring general ecological theory, while offering the precision of controlled experiments. Here we review the existing global-scale experiments conducted by stream ecologists and discuss the potential of this type of study for developing ecological theory and advancing our understanding of stream ecosystem functioning.

Key words: International collaboration, spatial scale, experimental manipulations, observational studies.

RESUMEN

Redes coordinadas a escala global como herramienta para explorar el funcionamiento de los ecosistemas fluviales

Los estudios ecológicos individuales, aunque adecuados para testar hipótesis y desarrollar la teoría, proporcionan información específica para un sitio o región en concreto, que es difícil de extrapolar para realizar generalizaciones. Los problemas globales que existen hoy en día (p.ej., el cambio climático, la pérdida de biodiversidad, las especies invasoras o la degradación de hábitats) requieren que reconsideremos qué métodos son los más apropiados para poder entender los patrones y procesos ecológicos a gran escala. El meta-análisis es una técnica que se usa a menudo para este propósito, ya que es un método cuantitativo que permite revisar, integrar y resumir gran número de estudios independientes. Sin embargo, la robustez de un meta-análisis depende de la de los estudios individuales que incluye, y los problemas de escala y metodología no pueden ser controlados retrospectivamente. Una técnica alternativa y emergente es la de los experimentos coordinados a escala global, realizados por múltiples grupos de investigación en diferentes zonas del mundo de manera paralela. Estos experimentos tienen la ventaja de abordar cuestiones globales y explorar la teoría ecológica, al mismo tiempo que ofrecen la precisión de los experimentos controlados. Aquí revisamos los experimentos a escala global que han sido llevados a cabo por ecólogos fluviales y discutimos el potencial de este tipo de estudios para desarrollar la teoría ecológica y mejorar nuestro conocimiento del funcionamiento de los ecosistemas fluviales.

Palabras clave: *Colaboración internacional, escala espacial, manipulaciones experimentales, estudios observacionales.*

THE SCALE ISSUE IN ECOLOGY

As stated by Simon Levin in his seminal paper in *Ecology*, 'when we observe the environment, we necessarily do so on only a limited range of scales' (Levin, 1992). Our capacity to examine ecological patterns and processes is frequently limited in spatial extent because of logistic and financial constraints. This is particularly true for community and ecosystem ecologists, who typically take a 'bottom-up' approach using small-scale experimental manipulations and field observations to infer patterns and processes at larger scales, in contrast to the 'top-down' perspective of macroecologists (Denny & Benedetti-Cechi, 2012).

Single-site experimental studies have contributed significantly to our understanding of ecological phenomena over the past few decades (Fraser *et al.*, 2013). However, our capacity to extrapolate the results of individual experiments or single-site observations to other sites is seriously limited because ecological systems vary substantially at different spatial scales according to multiple environmental gradients (Borer *et al.*, 2014). This limitation is remarkable, because many of the current and forecast anthropogenic environmental problems occur at broad scales, often globally. For example, the expansion of land area under agriculture is promoting the eutrophication of ecosystems world-wide (Tilman *et al.*, 2009); biodiversity is declining globally at alarming rates (Butchart, 2010), with demonstrated effects on the performance of ecosystems (Cardinale *et al.*, 2012); and deforestation across the world is altering the climate and the global carbon cycle (Bala, 2007). Understanding the functioning of ecosystems and the effects of these environmental drivers thus demands approaches that deal with their global nature and complexity.

TOOLS FOR EXPLORING GLOBAL-SCALE ECOLOGICAL PATTERNS AND PROCESSES

There is a diversity of tools used by ecologists to reveal general patterns from local-scale data (Borer *et al.*, 2014). The classical method is the literature review, more recently improved by a systematic and less subjective approach, where literature is critically appraised; however, it remains a qualitative approach. Meta-analysis, in contrast, is the quantitative synthesis and analysis of a collection of studies. Rather than taking into account the conclusions of individual studies (as systematic reviews do), the meta-analysis involves the combined datasets and compares 'effect sizes', which are estimates of the magnitude of the response to the experimental manipulation in each study (Osenberg *et al.*, 1999). This technique has been used by ecologists since the 1990s (Guervitch *et al.*, 2001) and has developed into one of the most powerful tools for describing ecological patterns. Another approach has been desktop description and analysis of diversity patterns, following collation of site information from many researchers world-wide (Vinson & Hawkins, 2003) or species-distribution and climate data accessible online (Pearson & Boyero, 2009). However, these approaches also have limitations: for example, the robustness of a meta-analysis or data collation is influenced by the robustness of individual studies or datasets, and is hampered by different methods and study designs (Borer *et al.*, 2014).

A more recent method for exploring global-scale ecological patterns is multi-site investigations, which are usually conducted by collaborative research networks or, in some cases, by non-researcher volunteers (Cohn, 2008). Collaborators may collect field data from multiple sites, often over extended periods, generating large datasets that allow predictive modelling of global-scale processes (e.g. modelling of carbon dioxide dynamics in different biomes by the FLUXNET network; Baldocchi *et al.*, 2001). Alternatively, a network may conduct manipulative experiments at multiple sites (e.g. examining climatic effects on litter decomposition rates in terrestrial habitats by the LIDET network; Gholz *et al.*, 2000). To date, large-scale manipulative networks have been rare, often restricted geographically (e.g. to Europe or North America), and have not always employed consistent experimental designs across sites (Fraser *et al.*, 2013).

WHAT'S BEHIND COORDINATED NETWORKS

As global issues require global approaches, a coordinated network should ideally encompass multiple sites across most continents. Clearly, the more dispersed the sites, the greater the potential for identifying general patterns, or for understanding the mechanisms underlying such patterns (Fraser *et al.*, 2013). Networks are typically led by a coordinator and core team, and the work is conducted by different researchers or teams at different locations, helping to avoid many of the logistic and financial problems inherent to large-scale studies.

To make sure that the same methodology is employed throughout, the coordinator provides an experimental protocol to all the collaborators, who in the early stages will comment on the protocol and clarify its details as necessary. The protocol must be very detailed, to avoid differences in its interpretation and execution. While unforeseen differences can be expected, these will be much smaller than differences between separate studies conducted individually by different researchers and using different methodologies. Pro-formas for data collection (e.g., spreadsheets) are provided to all participants to ensure standardisation of data recording and ease of subsequent processing. Once the experiments have been conducted at all sites, collaborators send their datasets to the coordinator, who organises data analysis and production of the results. The coordinator and core team then produce a first draft of a paper or papers for publication, which are circulated for comment by the entire network.

THE ROLE OF COORDINATED NETWORKS IN STREAM ECOLOGY

Coordinated networks have been rare in stream ecology. To our knowledge, the first large-scale network was 'RivFunction', which mainly explored effects of stream trophic status and riparian modification on leaf litter decomposition rates at >200 sites across nine ecoregions in Europe (Chauvet *et al.*, 2016). Litter decomposition was examined because of its key role in streams, and it responded consistently to nutrients across ecoregions in a humped-shaped manner: decomposition rates dramatically decreased at both extremes of the nutrient gradient as a result of nutrient limitation at one end, and toxic effects at the other end (Woodward *et al.*, 2012). Effects of riparian modification on leaf litter decomposition were less consistent because different types of change in riparian forests were examined in different European regions (e.g. eucalypt or conifer plantations, pastures, or forest clear cutting; Ferreira *et al.*, 2006; Hladyz *et al.*, 2011).

'BioCycle' is another example of coordinated network that focused (partly) on stream ecosystems. It encompassed five study sites in different biomes, four in Europe (subarctic, boreal, temperate and Mediterranean) and one in South America (tropical). Exploring effects of plant biodiversity loss on rates of litter breakdown and nutrient recycling in forests and streams, it for the first time produced evidence that nitrogen transfer between litter types was a likely mechanism underlying biodiversity effects on decomposition, with strikingly consistent patterns across biomes (Handa *et al.*, 2014).

Our network, recently named 'Global Lotic Breakdown Experiments (GLoBE) Network', has focused on global patterns and determinants of leaf litter decomposition in streams, and on latitudinal gradients of diversity of litter-feeding detritivores. Decomposition experiments encompassed 22-24 sites located across 90° of latitude on six continents, and demonstrated a major effect of temperature on microbial decomposition across latitudes, decreasing detritivore activity towards the tropics (Boyero *et al.*, 2011a), and important influences of water chemistry and litter quality and diversity (Boyero *et al.*, 2016). Concomitantly, observational studies conducted at >150 sites in 17 regions across the world showed that detritivores were more abundant and species rich at higher latitudes (Boyero *et al.*, 2012) in relation to environmental gradients as well as variation in biological processes such as dispersal (Boyero *et al.*, 2011b; Boyero *et al.*, 2015).

ONTOGENY OF THE GLoBE NETWORK

We established the network in 2006, with the aim of resolving some inconsistencies found in the literature regarding the role and nature of leaf litter decomposition in streams at different parts of the world. Following early research on decomposition (e.g. Kaushik & Hynes, 1971; Cummins *et al*., 1973), it had been widely accepted that headwater streams are heterotrophic systems and leaf litter is a major resource. This leaf litter is broken down by microorganisms and detritivores, with effects that propagate through detritivores to predators (Wallace, 1997). However, a study conducted in the 1990s at three sites in north and central America suggested that detritivores were only important at the temperate sites, with decomposition mostly driven by microorganisms at a tropical site in Costa Rica (Irons *et al*., 1994). Further studies reported similar results for other tropical sites such as Colombia (Mathuriau & Chauvet, 2002), and very low numbers and species richness of litter-feeding detritivores at several tropical locations such as Hong Kong (Dudgeon & Wu, 1999) and Kenya (Dobson et al., 2002).

The findings were not consistent with our observations in the Australian wet tropics, where litter-feeding detritivores were prominent in streams (Pearson *et al*., 1989; Cheshire *et al*., 2005). This inconsistency, and the scarcity of relevant tropical studies, suggested that a global study was necessary to determine whether detritivores were generally scarce in the tropics, and how their pattern of distribution might affect leaf litter decomposition. We commenced with a small-scale comparison between streams in central America and northern Queensland (Camacho *et al*., 2009), then established a network of colleagues who represented a wide latitudinal gradient globally. Initially, the network included 27 regions located in all continents except Antarctica: 6 regions were located in north and central America, 8 in south America, 4 in Europe, 1 in Africa, 4 in Asia, and 4 in Oceania. Subsequently, researchers from other regions have joined the

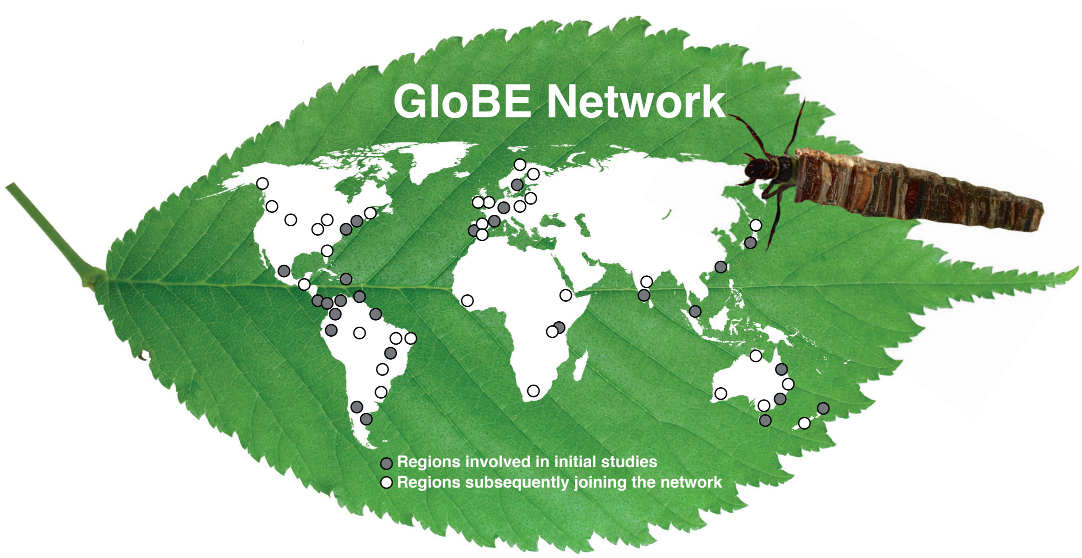

Figure 1. World map represented by a leaf being eaten by a caddisfly larva, showing the location of regions involved in the GLoBE Network. Leaf image purchased at https://www.dreamstime.com/ (Royalty free licence). Caddisfly image clipped from https://www.flickr.com/photos/aquaticinsects_of_central_virginia/8347124425/ (author, Bob Henricks; allowed for distribution and transformation under the following licence: https://creativecommons.org/licenses/by-sa/2.0/). *Mapa del mundo representado por una hoja que está siendo consumida por una larva de tricóptero, donde se muestran las regiones que forman parte de la Red GLoBE. Imagen de la hoja comprada en https://www.dreamstime.com/ (Royalty free licence). Imagen del tricóptero modificada de https://www.flickr.com/photos/aquaticinsects_of_central_virginia/8347124425/ (autor, Bob Henricks; permitida su distribución y modificación mediante la licencia: https://creativecommons.org/licenses/by-sa/2.0/.*

Figure 2. Steps followed by GLoBE partners involved in the leaf litter decomposition study described in the text. Photos: A, E, F, Luz Boyero; B top, free image from https://bossfight.co; B bottom, C, Tomoya Iwata (with permission); D, Ricardo Albariño (with permission). *Pasos que siguieron los colaboradores de GLoBE en el estudio de descomposición que se describe en el texto. Fotos: A, E, F, Luz Boyero; B arriba, imagen gratuita de https://bossfight.co; B abajo, C, Tomoya Iwata (con permiso); D, Ricardo Albariño (con permiso).*

network, which currently includes 59 regions: 14 in north and central America, 13 in south America, 12 in Europe, 5 in Africa, 6 in Asia and 9 in Oceania (Fig. 1).

PROTOCOL FOR A GLOBAL EXPERIMENT: AN EXAMPLE

Here we briefly illustrate the procedure followed in one of our global studies, which explored patterns of variation in leaf litter decomposition rates across latitudes. This study was designed to test several hypotheses regarding the influence of different environmental factors, as well as the relative role of microorganisms vs. detritivores, on decomposition rates across latitudes. Twenty-four regions were involved in the study, and one stream site was selected in each region, all of them draining forested watersheds experiencing little human influence. At each site we measured a set of environmental variables that we predicted would influence decomposition rates, the most important being temperature and pH (Fig. 2A).

Each partner conducted two parallel assays. The first one used leaves of a single tree species, *Alnus glutinosa* (L.) Gaertn., which has been used widely in decomposition experiments; this allowed us to examine patterns related to environmental variation and decomposer communities, without any influence of leaf traits. In the second assay we used mixtures of leaves from local species (which differed at each site), and we further looked at the effects of leaf quality and diversity on decomposition rates. In both cases, dry pre-weighed senescent leaves were introduced in coarse- and fine-mesh bags (Fig. 2B), which were incubated in streams. Replicates were collected after different periods of time, generally 2, 4 and 6 weeks (Fig. 2C), and the remaining leaf material was dried and weighed in the laboratory (Fig. 2D). Data sheets were prepared, which included initial and final leaf mass data at different times as well as environmental data (Fig. 2E), and sent to us for analysis and writing of manuscripts, which were subsequently reviewed by all partners until a final version was published (Fig. 2F).

A PROMISING FUTURE FOR NETWORKS

Currently, several coordinated experiments are being conducted over broad geographic areas. The 'CELLulose Decomposition EXperiment in streams and riparian zones across the Earth's major biomes' (CELLDEX) is investigating rates of decomposition of cellulose fabric (Tiegs *et al.*, 2013), with the aim of establishing baseline data to track changes in decomposition in the context of global environmental change (Scott Tiegs, pers. comm.). The '1000 Intermittent Rivers Project' is assessing the role of intermittent rivers and ephemeral streams globally in terms of nutrient dynamics and CO_2 release (http://1000_intermittent_rivers_project.irstea.fr). The project 'Biodiversity and biogeography of stream litter associated microbes across the globe by MiSeq high-throughput sequencing (GloFun)" is investigating global diversity patterns in stream microbial assemblages using Next-Generation Sequencing techniques (Seena Sahadevan, pers. comm.). The 'International Eucalypt Project' is examining functional responses of stream ecosystems to the worldwide replacement of native forests by plantations of *Eucalyptus globulus* (Verónica Ferreira, pers. comm.). The GLoBE project 'Decomposition and Diversity in streams: a global experiment' (DecoDiv) is exploring how plant functional diversity affects decomposition rates through different effects on dominant decomposer communities across climatic gradients. Lastly, the DOMIPEX and AGRHYDROM collaborative projects, carried out by young researchers of the Iberian Association of Limnology (AIL), are examining patterns of variation in carbon uptake and metabolism and the combined effects of agriculture and seasonal hydrology on dissolved organic matter, respectively, across European streams.

The current existence of all these coordinated networks and global studies is promising, as it will surely advance our understanding of how key freshwater ecosystem processes are affected by multiple biological and environmental factors, and how such processes are likely to change as a result of phenomena related to global change. Even if the creation and coordination of global coordinated networks is a challenging and time-consuming task (e.g. identifying and recruiting network members who have the logistic and financial capability to complete experiments, ensuring universal application of the protocol, moving materials between countries, determining authorship within each regional team), modern rapid communication overcomes some difficulties. The undertaking is also very rewarding, not only in generating globally important results but also in stimulating new research at many sites and in sharing common purpose, thereby improving research approaches and outcomes.

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