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Estimating heterotrophic respiration at large scales: challenges, approaches, and next steps

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Abstract. Heterotrophic respiration (HR), the aerobic and anaerobic processes mineralizing organic matter, is a key carbon flux but one impossible to measure at scales significantly larger than small experimental plots. This impedes our ability to understand carbon and nutrient cycles, benchmark models, or reliably upscale point measurements. Given that a new generation of highly mechanistic, genomic-specific global models is not imminent, we suggest that a useful step to improve this situation would be the development of "Decomposition Functional Types" (DFTs). Analogous to plant functional types (PFTs), DFTs would abstract and capture important differences in HR metabolism and flux dynamics, allowing modelers and experimentalists to efficiently group and vary these characteristics across space and time. We argue that DFTs should be initially informed by top-down expert opinion, but ultimately developed using bottom-up, data-driven analyses, and provide specific examples of potential dependent and independent variables that could be used. We present an example clustering analysis to show how annual HR can be broken into distinct groups associated with global variability in biotic and abiotic factors, and demonstrate that these groups are distinct from (but complementary to) already-existing PFTs. A similar analysis incorporating observational data could form the basis for future DFTs. Finally, we suggest next steps and critical priorities: collection and synthesis of existing data; more in-depth analyses combining open data with rigorous testing of analytical results; using point measurements and realistic forcing variables to constrain process-based models; and planning by the global modeling community for decoupling decomposition from fixed site data. These are all critical steps to build a foundation for DFTs in global models, thus providing the ecological and climate change communities with robust, scalable estimates of HR.

Key words: carbon cycle; heterotrophic respiration; modeling.

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Introduction: Heterotrophic Respiration and its Scaling

Heterotrophic respiration (HR) is the respiration rate of heterotrophic organisms (animals and microbes) integrated over ground or water area and through time (Chapin et al. 2006). The earliest published references to HR at ecosystem scales come from Odum (1956, 1959), and subsequently other authors applied this term to terrestrial ecosystems in a manner fully consistent with current usage (Kira and Shidei 1967, Woodwell and Whittaker 1968).

HR comprises a large and relatively uncertain component of ecosystem to global-scale carbon (C) cycles. In most terrestrial ecosystems, HR and net primary production (NPP) are the dominant fluxes determining the overall C balance; published data range widely, but annual HR is generally 48–99% of NPP in published studies (Fig. 1), varying two orders of magnitude from 11 to 1050 $gC \cdot m^{-2} \cdot yr^{-1}$ at the ecosystem scale. Global HR is generally estimated to be 51–57 Pg C/yr (Potter and Klooster 1998, Bond-Lamberty and Thomson 2010*c*, Hashimoto et al. 2015), a flux 5–6 times larger than annual anthropogenic emissions (Le Quéré et al. 2014). In general, regional- to global-scale HR has been correlated with mean annual temperature and precipitation (Wang et al. 2010). It is thus critical to understand how HR will respond to future climate changes, as models suggest it will strongly influence the dynamics of the global C cycle and climate system (Friedlingstein et al. 2006).

The high uncertainty of terrestrial HR, at scales from the measurement chamber (<1 m^2) to the global flux, comes from a number of sources. As a by-product of microbial growth and maintenance (Luo and Zhou 2006), HR is influenced by a wide variety of processes including mortality (from individual parts to entire populations killed by disturbance), grazing, and poorly understood soil stabilization mechanisms (Wynn et al. 2006, Harmon et al. 2011). In addition, partitioning the soil-to-atmosphere C flux, the dominant component of HR in most ecosystems, into its autotrophic and heterotrophic components has significant uncertainties for both methodological and biological reasons (Bond-Lamberty et al. 2004, Baggs 2006, Ngao et al. 2007). This translates into high spatial and temporal heterogeneity in HR fluxes, and significant uncertainty in upscaled estimates (Kim et al. 2010, Leon et al. 2014).

Unlike most other major C fluxes, HR cannot be directly measured at scales larger than a relatively small chamber. Thus, for any spatial domain larger than roughly a square meter, it must be either computed as a residual (e.g., in eddy covariance estimates as the difference between net ecosystem exchange and gross primary production, GPP), estimated from statistically upscaled point measurements, or derived using models with little ecological or biological process-level fidelity (Schimel 2013). This results in severe spatial and temporal scale mismatches between in situ HR observations and HR estimates from global Earth System Models (ESMs), limiting model benchmarking and analysis (Shao et al. 2013).

Ecosystem- to global-scale models, the latter including ESMs, generally simulate HR using relatively simple, first-order kinetics, typically scaling a base respiration rate by C pool size(s), soil temperature, and soil moisture. This semimechanistic formulation implicitly incorporates microbial physiology (Schimel 2013), and presumably future ESMs will include more explicit treatment of microbial dynamics (Wieder 2014). More sophisticated models such as DAMM (Davidson et al. 2012) that combine Michaelis–Menten kinetics and classic Arrhenius functions are another, promising way forward, but will depend on robust parameterizations that are spatially and temporally variable. Thus, there is a clear need for better, data-driven HR estimates at tower to pixel scales (i.e., larger than can be observed directly) to serve as an intermediate step between observations and future highly mechanistic models of, for example, soil physical heterogeneity and micro-organisms (Schmidt et al. 2011).

Decomposition Functional Types as an Intermediate Step

One intermediate step toward upscaling HR and better representing its underlying processes would be DFTs, "decomposition functional types" characterizing the behavior and sensitivities of heterotrophic-derived C fluxes, in particular as related to C turnover time. This approach would build on a long history of PFTs (plant functional types) and EFTs

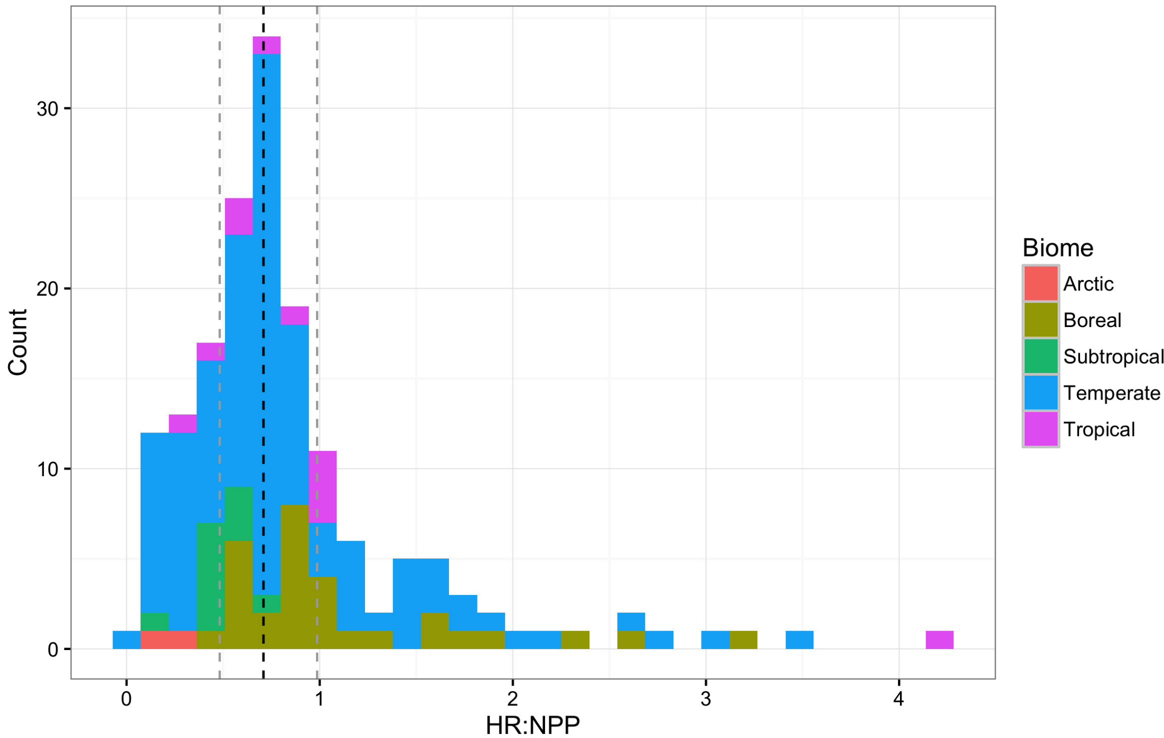

Fig. 1. Summary of published studies of soil heterotrophic respiration (HR) relative to net primary production (NPP), by biome. Vertical dashed lines show median of 0.71 (black line, N = 165) and 25% and 75% quantiles (gray). Data from version 20150826a of a global soil respiration database (Bond-Lamberty and Thomson 2010*a*).

(ecosystem functional types) in ecological and Earth system modeling. PFTs have been used extensively (see references in Bonan and Levis 2002) in both ecology and ecological modeling (Bormann and Likens 1979, Chapin et al. 1996), as an effort to simplify complex ecosystems into generalizable—and not incidentally, parameterizable—units. Efforts have also been made to define satellite-derived EFTs (Alcaraz-Segura et al. 2013) characterizing regional patterns of ecosystem function based on the magnitude, variability, and timing of canopy primary production. Both PFTs and EFTs can be highly correlated with functional characteristics at the ecosystem scale (Welp et al. 2007, Kuiper et al. 2014) that are useful for, and highly relevant to, models.

Robust, clearly defined DFTs would be conceptually analogous to PFTs and EFTs. Their goal would be to capture important differences in metabolism, dynamics, and abiotic response, particularly with respect to the integrated HR flux at the ecosystem (or larger) scale. DFTs would be complementary to PFTs and EFTs, but not necessarily correspond to their spatial or functional distribution. In addition to predicting the *mean* of these properties, DFTs would ideally usefully predict *distributions* and/or *likelihoods,* as well as how these properties vary in space and time. For example, the temporal variability in turnover times might vary more in DFTs associated with forested regions, compared to those associated with grasslands, because stochastic disturbances greatly increase the amount of decomposing wood in the former ecosystems. Alternatively, DFTs might vary significantly according to soil texture, such as sandy and clayey (Wynn et al. 2006, Haddix et al. 2011), or soil mineralogy (Lawrence et al. 2015) because of differences in C stabilization mechanisms. Because we expect that DFTs will be affected by both plant and soil properties, we expect they will be spatially distinct from PFTs; this assumption is tested below.

Toward a Bottom-up Identification of DFTs

How would meaningful DFTs be derived or identified? A number of previous studies have found that objective, bottom-up (i.e., data-driven) analyses produce results similar to those of subjective, top-down (i.e., expert opinion) ones (Díaz et al. 1992, Chapin et al. 1996). Initial top-down analyses based on expert opinion offer undeniable benefits in terms of hypothesis generation, motivating researchers to gather data necessary to test them. Nonetheless we suggest that the top-down option is poorly suited for identifying DFTs, given our relatively poor understanding of the highly variable soil processes and microsites controlling HR emissions (Davidson et al. 2014), compared to the depth of understanding for aboveground processes in plants, for example. In addition, by their nature top-down expert analyses are subjective, and thus neither reproducible nor well suited for drawing inferences from large volumes of data.

In contrast, a robust, bottom-up analysis of HR dynamics would control for and elucidate many different factors to specify DFTs. This would help generate insights and hypotheses for field experimentalists; be useful for up- and down-scaling data and model results; and ultimately provide a platform for model development and validation. Data-driven analyses are routinely used to generate hypotheses and identify unexpected relationships between driving variables and dependent variables (e.g., Carvalhais et al. 2014), and a DFT analysis could quantify variance, identify representative sites for particular domains of interest, and support model uncertainty quantification for HR processes.

A critical question with respect to DFTs is what the object(s) of analysis would be, as this choice will affect our a priori selection of traits, approach or algorithm, and final data set structure and size. Potential candidates include carbon turnover rates (Carvalhais et al. 2014); the relative contribution of HR sources (i.e., from mineral soil, organic matter, aboveground dead wood, or other); the relative influence of bacteria and fungi on HR (Strickland and Rousk 2010, Waring et al. 2013); the balance between aerobic and anaerobic processes; the annual flux of HR to the atmosphere, and/or its ratio to NPP (Fig. 1) or detritus production (Noormets et al. 2015); the temperature and moisture sensitivities (and thresholds) of HR fluxes; carbon use efficiency at a variety of scales (Eiler et al. 2003, Sinsabaugh et al. 2013, Li et al. 2014); and the temporal dynamics of HR processes (cf. Alcaraz-Segura et al. 2013). These are all characteristics that can be expected to encapsulate the HR response to a wide range of abiotic drivers and biotic processes, and while they could be analyzed separately, an ideal analysis and classification would consider them all simultaneously.

Ancillary and/or independent variables in a DFT analysis could include a wide variety of field measurements, remote sensing observations, and a priori knowledge. For example, the dominant decomposers groups (Högberg and Read 2006); vegetation type and structure (part of PFTs), especially fine root data stored in databases such as TRY (Kattge et al. 2011); depth of a wide variety of processes (e.g., rooting, thawing, wetting, root exudation) and soil properties (Hengl et al. 2014); the expression of functional attributes related to soil taxon; stoichiometry constraints; vegetation phenology and seasonality (a component of EFTs); temporal lags between organic matter inputs and HR fluxes; the diversity of active soil enzymes related to HR; atmospheric deposition rates of fertilizers and pollutants (Vet et al. 2014); short- and long-term climate drivers (e.g., Hijmans et al. 2005); disturbances (van der Werf et al. 2006, Harmon et al. 2011); and management (Noormets et al. 2015) and land-use history (Arevalo et al. 2011). In addition, a growing body of research suggests that the presence of arbuscular mycorrhizae vs. ectomycorrhizae exerts both direct and indirect effects on soil C cycling (Ekblad et al. 2013, Soudzilovskaia et al. 2015) and ecosystem respiration (Vargas et al. 2010), spurring the development of global databases of such properties. Recent high-resolution global soil data sets (e.g., Hengl et al. 2014) would provide information about soil properties; soil order, in particular, might condense a great deal of information into a simple categorical variable. This (probably incomplete) list of factors that might be useful in an HR upscaling analysis can be grouped into (1) data that are imperfect but straightforward to obtain at the global scale (e.g., climate, soils,

(a)

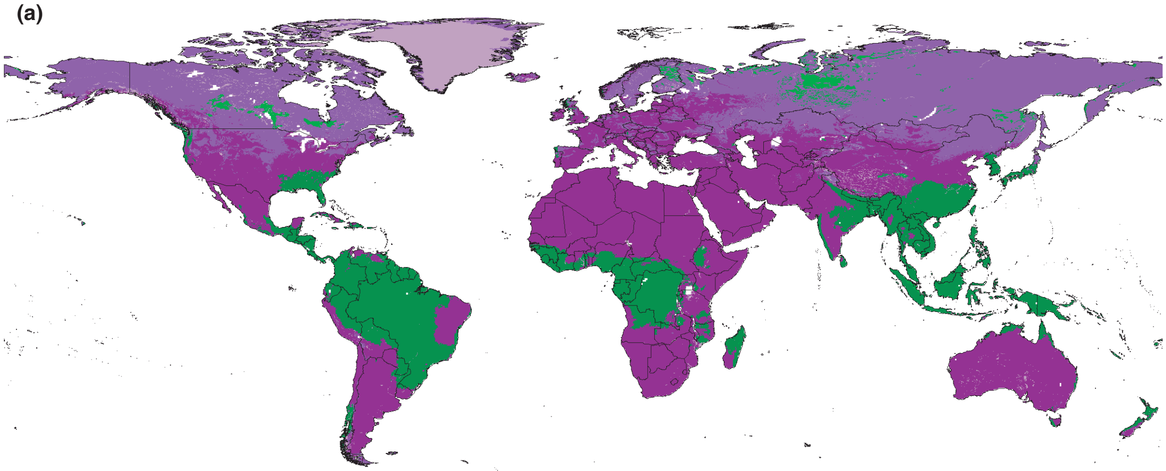

Fig. 2. Examples of clustering analysis for delineating decomposition functional types from 11 global climatic, edaphic, ecosystem carbon flux, and topographic characteristics. Randomly colored maps show the (a) five and (b) 50 most-different land regions according to simultaneous consideration of all 11 variables. The map in (c) is the same as the 50-region map, but is colored using the three dominant and orthogonal factors derived from PCA as shown in Table 1. Spatial resolution is 4 km^2.

vegetation, land-use history data); and (2) data for which no or very limited global data sets currently exist (everything else).

A variety of algorithmic approaches could be used for such an analysis. Machine learning, for example, includes decision trees, neural networks, and Bayesian classifiers (Jordan and Mitchell 2015). These methods are typically robust to overfitting and correlated predictors, probabilistic (as opposed to deterministic), data-driven, and bottom-up: the algorithms know nothing about biology, for better and for worse, and generally start with minimal or no predefined model structures. Multivariate geographic clustering, used in the delineation of ecoregions (Hargrove and Hoffman 2004) and the design of the NEON network (Keller et al. 2008), offers another approach that might be well suited for identifying and assigning DFTs. For example, the *k*-means algorithm (Hartigan 1975) equalizes the full multidimensional variance across clusters calculated from an arbitrary number of observation vectors (here, HR and its candidate predictors). It has the advantage of not depending on a single dependent variable, and could thus optimize for a variety of HR-related characteristics simultaneously (see above).

Exploring Possible DFT Definitions: Methods and Results

To illustrate the possibilities of such an approach for delineating DFTs, we conducted a cluster analysis based on 11 global climatic, edaphic, modeled HR and GPP fluxes, and topographic characteristics. Figure 2 shows the five and 50 most-different land regions when considering all these variables simultaneously. Climate data consisted of decadal mean and standard deviations of temperature and precipitation from WorldClim (Hijmans et al. 2005). Edaphic variables included water holding capacity, bulk density, and carbon and nitrogen content in soils (Global Soil Data Task Group 2000). Decadal mean annual fluxes of HR and GPP were obtained from a contemporary simulation of the Community Land Model version 4.0 (CLM4.0) (Oleson et al. 2010). A unitless compound topographic index (CTI), calculated from GTOPO30 (U.S. Geological Survey 1996), was also included in the analysis. These data were analyzed using a custom-developed scalable and parallel implementation of the *k*-means clustering algorithm on high-performance computing systems (Hoffman et al. 2008, Kumar et al. 2011).

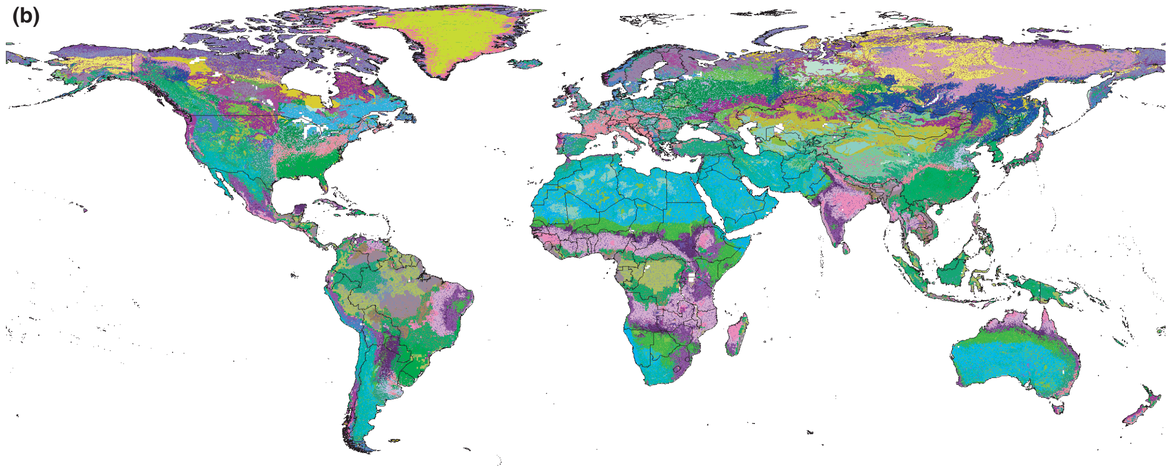

Fig. 2. Continued.

At a coarse level of division, large and cohesive regions (Fig. 2a) emerge from the data and algorithm: five broadly defined DFTs that include tropical and subtropical forested regions (green); deserts and mid-latitude savanna, grassland, and forest regions (yellow); high latitude and formerly glaciated regions (red); high latitude wetland or peatland areas (blue); and glaciers and inland lakes (cyan). A finer level of division, for example the 50 clusters shown in random colors in Fig. 2b, better resolves the differences among potential DFTs. Here, large deserts share a single DFT, with some heterogeneity apparent in the Sahara Desert and the Middle East. Forested high latitudes in Alaska and Siberia share a DFT, which is distinct from those delineated for areas covered by boreal forests at upper mid-latitudes. With 50 clusters, the DFT defined for the region of subtropical forests in the southeastern United States is different from those co-located with tropical forests in South America and Africa, and most of the land area of the Indo-Pacific Islands shares a DFT with only the very densest tropical forests in the western Amazon Basin, where Peru, Colombia, and Brazil meet.

To further investigate the relationships between the factors chosen for our initial cluster analysis, we performed a Principal Components Analysis (PCA) on the 11 variables for the 50 cluster centroids. The first three principal components (PCs) explained 78.2% of the total variance (Table 1). PC1 was dominated by precipitation, HR, GPP, and temperature; PC2 was dominated by soil nutrients and bulk density; and PC3 was dominated by soil properties and topography. For insight into the similarity of adjacent regions or DFTs, Fig. 2c shows to what degree each PC dominates the various regions of Fig. 2b. In this analysis, soil physical properties (in red) provide a background setting for most of the globe, climate and plant productivity (blue) are strong drivers of variance in the tropics, and substrate and soil nutrients (green) are large in high latitude taiga and peatlands.

It is notable that DFTs do not simply overlap already-existing PFTs. Using the Mapcurves method (Hargrove et al. 2006), we compared the prototype map of 50 DFTs (Fig. 2b) with the 17-category global International Geosphere–Biosphere Programme (IGBP) Land Cover Classification (Belward 1996), which is commonly used to inform the spatial distribution of PFTs for land surface models. Mapcurves provides a goodness-of-fit (GOF) score that indicates the degree of spatial correspondence between polygons in two different maps. A map of those GOF scores, shown in Fig. 3, reveals that our prospective DFTs have large spatial overlap (>20%) with IGBP land cover classes in glacial regions, and relatively high overlap in some tropical forests and deserts. However, the darkening gradient in other regions shows declining spatial correspondence, supporting the idea that DFTs would offer a useful and complementary framework for segmenting decomposition and mineralization processes distinct from PFTs.

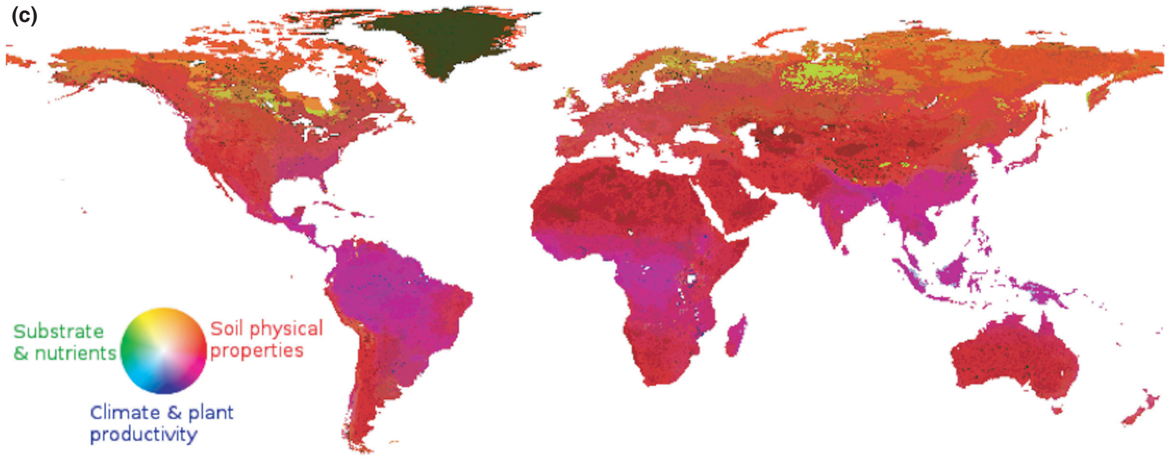

Fig. 2. Continued.

In summary, clusters identified by a similar analysis could form the basis for future DFTs, offering both a framework for upscaling measurements and a downscaling approach for integration of models and measurements (Hoffman et al. 2013). We emphasize that the results shown here draw only on modeled C fluxes; a more robust analysis would clearly depend heavily on observational data (Bond-Lamberty and Thomson 2010*a*, Wang et al. 2010).

Next Steps

We thus argue that a robust DFT analysis, and tentative DFT definitions, would be useful for both experimentalists and modelers. Such definitions would not be the final word, any more than Chapin et al. (1996) was the final word in PFTs, but would provide testable hypotheses for a wide range of field, laboratory, and modeling experiments, and identify weaknesses (whether spatial, temporal, disciplinary, or something else) in existing data networks (e.g., Baldocchi 2014), and our understanding of ecosystem- to global-scale C cycles.

For these reasons, we recommend extending the sample bottom-up analysis shown here (Fig. 2), aiming to produce a more robust definition of DFTs. Such analysis would make heavy use of observational databases of HR (Bond-Lamberty and Thomson 2010*b*, Wang et al. 2010, Hashimoto et al. 2015) other greenhouse gas fluxes (Kim et al. 2010, Turetsky et al. 2014), and soil factors such as texture, horizonation, or mineralogy (see, e.g., http://

Table 1. A principal components analysis was used to convert the 11 climate, edaphic, carbon flux, and topographic variables from the 50 cluster centroids into linearly uncorrelated variables or principal components (PCs). As shown here, the first three PCs, explaining 78.2% of the total variance, were retained and assigned labels and colors—blue, green, and red, respectively—based upon the contributing variables that loaded more than 25% onto each PC.

Climate and plant productivity		Substrate and nutrients		Soil physical properties	
Variable	Percentage	Variable	Percentage	Variable	Percentage
PC1	35.4	PC2	26.0	PC3	16.8
Precipitation, mean	48.7	Soil carbon content	66.8	Water holding capacity	60.4
Precipitation, SD	46.7	Soil N content	62.6	Soil bulk density	59.3
Heterotrophic respiration	43.1	Soil bulk density	31.1	Compound topographic index	−43.2
Gross primary production	42.9				
Temperature, SD	−30.6				
Temperature, mean	26.4				

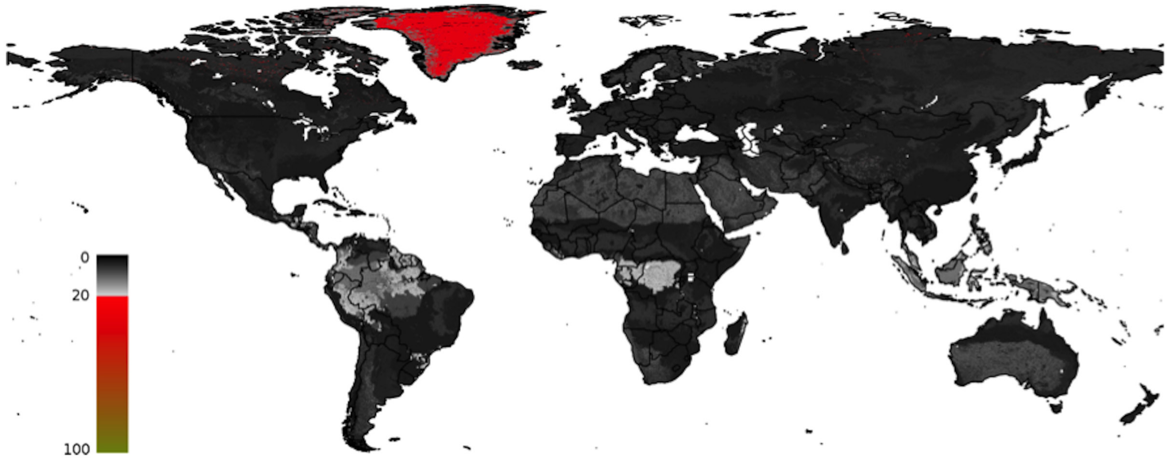

Fig. 3. Goodness-of-fit scores from the Mapcurves method (see text), indicating the degree of spatial correspondence between the 50-region prototype DFT map (Fig. 2b) and IGBP land cover classes. Regions with very high overlap (>20%) are shown in red; below 20%, light colored regions have high overlap and dark regions have low correspondence.

iscn.fluxdata.org/). A number of ancillary data sources are discussed above; we note in particular the spatially explicit TRY (Kattge et al. 2011) and Biomass and Allometry Database (BAAD, Falster et al. 2015) databases that might be usefully mined for predictors. A notable weakness with this approach is that observationally based HR estimates are biased toward "fast-cycling" C pools (Epron et al. 2009, Carvalhais et al. 2014). Given the relative paucity of soil isotopic data, comparisons and experiments will need to be carefully designed to assess this level of bias and how DFTs might mitigate this problem. Techniques such as *k*-means clustering can be sensitive to initial conditions, and careful testing and validation using techniques such as ensemble clustering (Jain 2010) will be necessary for robust DFT definitions.

Concurrently, a top-down initiative could hypothesize how key driving variables influence DFT prediction properties, and estimate how many DFT clusters will likely exist based on our a priori knowledge. The spatial distribution of likely driving variables could be used to create spatial predictions of DFTs, and these hypotheses could be tested locally. The results of these tests would be uploaded into a common database or repository (e.g., http://www.isric.org), available for testing and discussion of any hypothesized DFT classification (Fig. 4). We recognize that standardizing a data set structure would be challenging because HR-related information is heterogeneous in terms of the methods, corrections, and spatiotemporal domains. DFT data sets will contrast with current simpler data set structures for PFTs and ECTs; the former tend to segment biota by leaf physiology and carbon allocation (Bonan and Levis 2002), and the latter by phenology and carbon gain dynamics (Alcaraz-Segura et al. 2013).

How would DFTs be tested and validated? The machine-learning and clustering methods discussed above provide statistics on their performance, including against both the training data (used to build the model) and "out-of-bag" testing data (which are unknown to the model). Many other tests are possible: do the "borders" of clusters (DFTs) match up with known biotic and abiotic boundaries? How well do DFTs match PFTs, independent HR estimates (e.g., Hashimoto et al. 2015), total soil carbon (Hengl et al. 2014), and carbon turnover maps (Carvalhais et al. 2014)? Do the implied functional relationships make theoretical sense, and are they consistent with observations? Do they match field studies aimed specifically testing these hypotheses? Do DFTs significantly improve the performance of ecosystem to global-scale models at predicting the mean and spatial and temporal variations in HR?

If DFTs prove conceptually solid, operationally tractable, and effective in improving large-scale HR predictions, modelers will want to

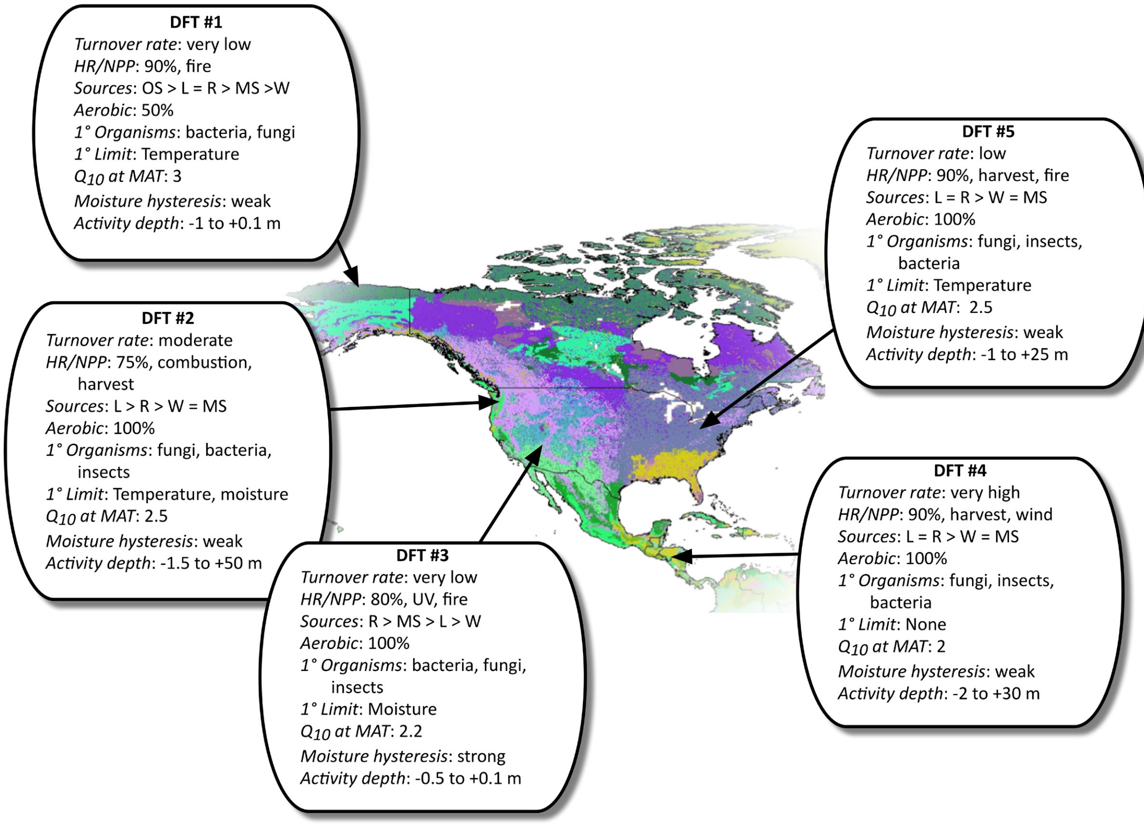

Fig. 4. Illustrative example of how a data-driven algorithmic approach to defining decomposition functional types (DFTs) could be combined with expert opinion and insight. The map is a subset of that generated by a machine-learning algorithm (cf. Fig. 2), while the boxed annotations represent (example) expert opinion about the algorithmic results. Properties include the average turnover rate; the HR/NPP ratio, indicating the percentage of NPP expected to be respired via HR vs. other processes; the sources of HR, listed in order of importance (L leafy litter; R dead roots; W wood; OS organic soil; and MS mineral soil); the estimated fraction of HR released as CO_2 as opposed to methane; the primary heterotrophs in order of importance; the primary environmental limitation(s); temperature sensitivity expressed as increase per 10 °C at the mean annual temperature; strength of the moisture hysteresis; and depth that HR occurs with minus values below the soil surface and positive values above it.

consider if, and how, they would be implemented in ESMs. Given the large uncertainties associated with global models' HR outputs (Shao et al. 2013), we hope that this will be an attractive possibility for the ESM community. Many such models already support multiple levels of nested, overlapping units: in the Community Land Model, for example, multiple PFTs currently share a single soil column, with this entire structure nested within sub-grid-cell land units and then grid cells (Oleson et al. 2013). But how DFTs might be incorporated into this structure, with site data specifying one or more relevant DFTs; how they might fit with trait-based modeling (Fisher et al. 2015) and other modeling approaches; and how they might be tested against simple microbial models (Wieder et al. 2013) are open questions.

Conclusions

In summary, we argue that the scientific community needs to synthesize, harmonize and incorporate relevant information to inform next-generation global models in order to reduce the uncertainty in regional to global quantification and forecasting of HR. We have suggested a first approach that could encapsulate information relevant to HR as DFTs, as well as next steps and priorities, including collection and synthesis of existing data; more in-depth analyses combining open data with rigorous testing of analytical results; using point measurements and realistic forcing variables to constrain process-based models; and planning by the global modeling community for decoupling decomposition from fixed site data.

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