## **Article**

## The three major axes of terrestrial ecosystem function

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Mirco Migliavacca<sup>1,2,55</sup>, Talie Musavi<sup>1</sup>, Miguel D. Mahecha<sup>1,2,3,4</sup>, Jacob A. Nelson<sup>1</sup>, Jürgen Knauer<sup>5,56</sup>, Dennis D. Baldocchi<sup>6</sup>, Oscar Perez-Priego<sup>7</sup>, Rune Christiansen<sup>8</sup>, Jonas Peters<sup>8</sup>, Karen Anderson<sup>9</sup>, Michael Bahn<sup>10</sup>, T. Andrew Black<sup>11</sup>, Peter D. Blanken<sup>12</sup>, Damien Bonal<sup>13</sup>, Nina Buchmann<sup>14</sup>, Silvia Caldararu<sup>1</sup>, Arnaud Carrara<sup>15</sup>, Nuno Carvalhais<sup>1,16</sup>, Alessandro Cescatti<sup>17</sup>, Jiquan Chen<sup>18</sup>, Jamie Cleverly<sup>19,20</sup>, Edoardo Cremonese<sup>21</sup>, Ankur R. Desai<sup>22</sup>, Tarek S. El-Madany<sup>1</sup>, Martha M. Farella<sup>23</sup>, Marcos Fernández-Martínez<sup>24</sup>, Gianluca Filippa<sup>21</sup>, Matthias Forkel<sup>25</sup>, Marta Galvagno<sup>21</sup>, Ulisse Gomarasca<sup>1</sup>, Christopher M. Gough<sup>26</sup>, Mathias Göckede<sup>1</sup>, Andreas Ibrom<sup>27</sup>, Hiroki Ikawa<sup>28</sup>, Ivan A. Janssens<sup>24</sup>, Martin Jung<sup>1</sup>, Jens Kattge<sup>12</sup>, Trevor F. Keenan<sup>6,29</sup>, Alexander Knohl<sup>30,31</sup>, Hideki Kobayashi<sup>32</sup>, Guido Kraemer<sup>3,33</sup>, Beverly E. Law<sup>34</sup>, Michael J. Liddell<sup>35</sup>, Xuanlong Ma<sup>36</sup>, Ivan Mammarella<sup>37</sup>, David Martini<sup>1</sup>, Craig Macfarlane<sup>38</sup>, Giorgio Matteucci<sup>39</sup>, Leonardo Montagnani<sup>40,41</sup>, Daniel E. Pabon-Moreno<sup>1</sup>, Cinzia Panigada<sup>42</sup>, Dario Papale<sup>43</sup>, Elise Pendall<sup>44</sup>, Josep Penuelas<sup>45,46</sup>, Richard P. Phillips<sup>47</sup>, Peter B. Reich<sup>44,48,49</sup>, Micol Rossini<sup>42</sup>, Eyal Rotenberg<sup>50</sup>, Russell L. Scott<sup>51</sup>, Clement Stahl<sup>52</sup>, Ulrich Weber<sup>1</sup>, Georg Wohlfahrt<sup>10</sup>, Sebastian Wolf<sup>14</sup>, Ian J. Wright<sup>44,53</sup>, Dan Yakir<sup>50</sup>, Sönke Zaehle<sup>1</sup> & Markus Reichstein<sup>1,2,54</sup> □

The leaf economics spectrum<sup>1,2</sup> and the global spectrum of plant forms and functions<sup>3</sup> revealed fundamental axes of variation in plant traits, which represent different ecological strategies that are shaped by the evolutionary development of plant species<sup>2</sup>. Ecosystem functions depend on environmental conditions and the traits of species that comprise the ecological communities<sup>4</sup>. However, the axes of variation of ecosystem functions are largely unknown, which limits our understanding of how ecosystems respond as a whole to anthropogenic drivers, climate and environmental variability<sup>4,5</sup>. Here we derive a set of ecosystem functions<sup>6</sup> from a dataset of surface gas exchange measurements across major terrestrial biomes. We find that most of the variability within ecosystem functions (71.8%) is captured by three key axes. The first axis reflects maximum ecosystem productivity and is mostly explained by vegetation structure. The second axis reflects ecosystem water-use strategies and is jointly explained by variation in vegetation height and climate. The third axis, which represents ecosystem carbon-use efficiency, features a gradient related to aridity, and is explained primarily by variation in vegetation structure. We show that two state-of-the-art land surface models reproduce the first and most important axis of ecosystem functions. However, the models tend to simulate more strongly correlated functions than those observed, which limits their ability to accurately predict the full range of responses to environmental changes in carbon, water and energy cycling in terrestrial ecosystems7,8.

Terrestrial ecosystems provide multiple functions (for example, resource use and potential uptake of carbon dioxide, among others) and ecosystem services on which society depends<sup>5</sup>. To understand and predict the response mechanisms of ecosystems as a whole to climatic and other environmental changes, it is crucial to establish how many and which functions need to be measured to obtain a good representation of overall ecosystem functioning. So far, the key functional axes that control the behaviour of terrestrial ecosystems have not yet been quantified<sup>5</sup>. This can be achieved by identifying associations between a comprehensive set of ecosystem functions measured consistently across major terrestrial biomes and a range of climatic conditions.

Here, we identify and quantity the major axes of terrestrial ecosystem functions and sources of variation along these axes. First, we characterize multiple ecosystem functions across major terrestrial biomes. Second, we identify the most important axes of variation of ecosystem functions using an exploratory analysis similar to that used for the global spectrum of plant forms and functions<sup>3</sup>. Third, we analyse which variables drive the variation along these axes, from a suite of climatic variables, and the structural and chemical properties of the vegetation. Fourth, we analyse the extent to which two state-of-the-art land surface models (models that simulate the states and exchange of matter and energy between the Earth's surface and the atmosphere) reproduce

A list of affiliations appears at the end of the paper.