Effects of climate legacies on above- and belowground community assembly

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Abstract
The role of climatic legacies in regulating community assembly of above- and belowground species in terrestrial ecosystems remains largely unexplored and poorly understood. Here, we report on two separate regional and continental empirical studies, including >500 locations, aiming to identify the relative importance of climatic legacies (climatic anomaly over the last 20,000 years) compared to current climates in predicting the relative abundance of ecological clusters formed by species strongly co-occurring within two independent above- and belowground networks. Climatic legacies explained a significant portion of the variation in the current community assembly of terrestrial ecosystems (up to 15.4%) that could not be accounted for by current climate, soil properties, and management. Changes in the relative abundance of ecological clusters linked to climatic legacies (e.g., past temperature) showed the potential to indirectly alter other clusters, suggesting cascading effects. Our work illustrates the role of climatic legacies in regulating ecosystem community assembly and provides further insights into possible winner and loser community assemblies under global change scenarios.

Keywords
animals, bacteria, ecological networks, fungi, paleoclimate, plants, terrestrial ecosystems

1 INTRODUCTION

Current climate is known to be one of the major environmental filters shaping above- and belowground community assemblies (Schleuning et al., 2016), as particular groups of species only occur under specific ranges of precipitation and/or temperature. Nevertheless, climatic conditions are dynamic and have been shown to shift profoundly over millennia. Consequently, paleoclimatic filtering might have left a strong signature on the current above- (plants and animals) and belowground (bacteria, fungi, protists, and soil invertebrates) community assemblies found within ecological networks across entire terrestrial ecosystems. Although such an argument is intuitive conceptually, the relative importance of paleoclimatic legacies (i.e., temperature and precipitation differences from the present to ~20,000 years ago; Fordham et al., 2017) compared with the current climate filtering in predicting the assembly of entire ecological network of above- and belowground communities has never been explicitly tested. Furthermore, no large-scale studies have addressed...
this important research question. Here, we tested the hypothesis that historical climatic legacies (hereafter “climatic legacies”) explain important parts of the variation in ecosystem above- and belowground community patterns found within ecological networks that cannot be accounted for by current climates.

Studies over the past two decades provide strong evidence that climatic changes, since the last glaciation about 10,000 years ago (Fordham et al., 2017), are partly responsible for the current distribution of plants, animals, and microbial communities in terrestrial ecosystems globally (Atkinson, Briffa, & Coope, 1987; Delgado-Baquerizo et al., 2017; Lyons et al., 2016; Partel et al., 2017; Svenning, Eiserhardt, Normand, Ordenez, & Sandel, 2015). Recent studies have also provided solid evidence that a knowledge of climatic legacies can improve our predictions of the current distribution of specific groups of organisms including plants and microbes (Delgado-Baquerizo et al., 2017; Partel et al., 2017; Schleuning et al., 2016). Much less is known on the role of climatic legacies in driving ecological networks of above- and belowground organisms. Plant- and soil-microbial communities comprise two components of the most important terrestrial food webs: aboveground and belowground. The first is essential for the provision of food and fiber and the second supports key soil processes such as litter decomposition and nutrient cycling, which in turn, supports plant productivity (De Vries et al., 2012; Hooper et al., 2000; Wardle et al., 2004). Because of their enormous functional importance, identifying new predictors that help explain the distribution of entire biotic community assemblies is one of the major endeavors in which scientists are immersed today. Moreover, future projections are conditional upon the past. Thus, a demonstrable link between climatic legacies and current ecosystem community assemblies found within ecological networks would improve our capacity to predict how entire ecosystem community assemblies might respond to forecasted climate change, and the extent to which climatic change might affect the myriad ecosystem services these communities provide.

Given the strong links between climatic legacies and the current distribution of particular groups of soil microbes and plants (Delgado-Baquerizo et al., 2017; Partel et al., 2017; Schleuning et al., 2016), we hypothesized that the past climates might have triggered the current above- and belowground community assemblies in terrestrial ecosystems, that is, the identity and abundance of coexisting multitrophic species within ecological networks that occur today. For example, locations with a positive anomaly in temperature or precipitation over the last 20,000 years might have resulted in a completely different biotic community assembly compared with locations with a negative anomaly or no change in temperature or precipitation, even if all these locations share the same current climate. If climatic legacies play a role in regulating the current network of ecological interactions, then climatic legacies might help to explain particular community assemblies that cannot be explained using only current climate data. This unexplained variation has hitherto generally been ascribed to stochasticity (e.g., Powell et al., 2015). Thus, climatic legacies might help us to explain why two locations with a similar current climate do not always lead to exactly the same community assembly.

We argue that Australia is one of the best locations on the Earth to identify the role of climatic legacies in driving current ecosystem community assembly for three reasons. First, Australia has a long history of aboriginal occupation (>60,000 years), characterized by a semisedentary, hunter-gatherer lifestyle (Hubble, Isbell, & Northcote, 1983). Compared with other continents, Australia has a relatively recent history of European occupation (~200 years), and therefore, a short history of intensive agriculture. Because of a short European history, >90% of Australia’s land mass is still occupied by native vegetation and <6% is arable. Therefore, compared with other continents, the network of ecological interactions in Australian ecosystems is more likely to resemble those that existed prior to large-scale agricultural management. Second, contemporary agricultural land use in Australia is predominantly livestock grazing and cropping, and statistical models are able to account for the impacts of both land uses on our conclusions. Finally, given its continental scale, Australia experienced a wide range of climatic legacies over the past 20,000 years, including both positive and negative anomalies in temperature and precipitation variables (see examples in Supporting Information Figure S1). Consequently, Australia provides enough statistical variability to enable us to answer our primary research questions.

Herein, we used a combination of ecological network analyses and statistical modeling to evaluate the relative importance of climatic legacies compared to current climates in predicting the relative abundance of particular ecological clusters of strongly co-occurring species. Intuitively, we would expect these clusters to include species across multiple trophic levels and to be good surrogates of exclusive ecosystem community assemblies. We also aimed to identify the most important climatic legacies explaining the relative abundance of these ecological clusters and describe the examples of specific species-species interactions within these clusters across different trophic groups (predator-prey) and associations (host-symbiont). To address our research questions, we used two independent datasets from Australia, which included >500 locations at both regional and continental scales. The first dataset, which included information, from 108 “natural” locations in eastern Australia on the composition of plant and animal species, was used to build an aboveground (plants and animals) correlation network. The second dataset, including 375 “natural” and 60 cultivated locations across mainland Australia, contained information on the composition of soil bacteria and eukaryotes (fungi, protists, and soil invertebrates). This dataset was used to build a belowground correlation network.

2 | MATERIALS AND METHODS

2.1 | Aboveground network

Our aboveground network study was conducted at 108 sites across a large area (~500 km²) of eastern Australia (Supporting Information Figure S1). This survey was undertaken in three seminatural woodland communities dominated by blackbox (Eucalyptus largiflorens),
white cypress pine (*Callitris glaucophylla*), and river red gum (*Eucalyptus camaldulensis*). These three communities include sites used extensively for livestock grazing, large areas dedicated to conservation (national parks, nature reserves), and smaller areas devoted to native forestry, but excluded any areas that were cultivated or supported crops. In these locations, we undertook multiple vegetation and animal surveys targeting grasses, forbs, woody plants, birds, mammals, reptiles, amphibians, and invertebrates (see Supporting Information Appendix S1 for sampling details).

### 2.2 | Belowground network

We used a subset of sample locations from the Biome of Australia Soil Environments (BASE) project (Supporting Information Figure S1) for our belowground network (soil bacteria, fungi, protists, and soil invertebrates). This subset includes data on the composition of bacterial, fungal, and eukaryotic communities across 439 locations belonging to “natural” (379) and agricultural (60) (wheat and cotton crops) ecosystems from Australia. Samples were collected between 2011 and 2014. In each location, a $25 \times 25$ m plot was established. Soil samples (top 10 cm) were collected according to the methods described in Bissett et al. (2016). The community composition of soil bacteria, fungi, protists, and soil invertebrates was determined using amplicon sequencing with the Illumina MiSeq platform (see Supporting Information Appendix S2 for details).

### 2.3 | Climate data

For all sites surveyed, we obtained six climatic variables for current climate and climate in the Last Glacial Maximum from the Worldclim database (www.worldclim.org) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These variables include mean precipitation (MAP), maximum and minimum temperature (MAXT and MINT), mean annual precipitation and temperature seasonality (PSEA and TSEA), and mean diurnal temperature range (MDR). We selected these six variables as they provide a good approximation of the quantity and variability of precipitation and temperature. In addition, these six variables did not suffer from strong multicollinearity (Pearson’s $r < 0.8$; Katz, 2006). In the case of Last Glacial Maximum climate, we used estimates provided by the Community Climate System Model (CCSM4; www.worldclim.org) (Bystriakova et al., 2014; Tallavaara, Luoti, Korhonen, Järvinen, & Seppä, 2015). We used data at a 2.5 min resolution (~4.5 km at Equator), as this is the highest resolution available for the Last Glacial Maximum period. Previous studies have demonstrated that the Last Glacial Maximum information used here largely resemble information coming from other climatic models (Delgado-Baquerizo, Reich, Garcia-Palacios, & Milla, 2016) and spatial and temporal resolutions (Delgado-Baquerizo et al., 2017).

### 2.4 | Climatic legacies

Climatic legacies were calculated as the differences between an estimate of six climatic variables (amount and variability in precipitation and seasonality) 20,000 ybp and another estimate for these variables at the present day (Fordham et al., 2017) as shown in Delgado-Baquerizo et al. (2017). In particular, the climatic legacy for each climatic variable is calculated as the mathematical difference in the values for each climatic variable from Last Glacial Maximum and current climates (e.g., Annual precipitation$_{\text{Current climate}}$–Annual precipitation$_{\text{Last Glacial Maximum}}$) for each site. This difference provides us with a measure of climatic legacies; increases, declines or a lack of change in a particular climatic condition with time in each of the sites surveyed from the different datasets. A recent cross validation of the climatic legacy indexes used here is given in Appendices 1–3 in Delgado-Baquerizo et al. (2017) and Supporting Information Appendix S1 in Delgado-Baquerizo, Reich, et al. (2016). Note that the climatic legacy index used here is based on the differences between two single snapshots in time (Current vs. Last Glacial Maximum climates); thus, calculation of climate legacy comes with a number of inherent and important assumptions (Fordham et al., 2017). For example, although we assume that change in precipitation and temperature gradually occurred with time during last 21,000 years, we would like to acknowledge that most abrupt changes in climate occurred prior to 10,000 YBP (see Fordham et al., 2017). Even so, our climatic legacy index still allowed us to address our research question of whether the signature of climatic legacies on the network of interactions of aboveground and belowground can still be detected today. Further discussion on this point is available at Appendices 1–3 in Delgado-Baquerizo et al. (2017).

### 2.5 | Soil properties and current management

Soil properties including texture (% sand content), pH, soil C, and P were available from the two datasets used here (Supporting Information Appendix S3). Current management including intensity of grazing by cattle and the incidence of cropping (only applicable to the belowground dataset) was included in our statistical models (see below) to account for impacts from recent management in the network of interactions of aboveground and belowground. We used cattle density as our proxy of current management as grazing by cattle is one of the major drivers of grazing-induced degradation in Australia, over the past 200 years (see Supporting Information Appendix S3 for details).

### 2.6 | Network analyses

Network analyses were conducted separately for the aboveground and belowground network Australian datasets. In both cases, we identified ecological clusters of strongly associated taxa using correlation networks (“co-occurrence network”) and the following protocol. Our aboveground network contained 1,280 nodes (species of vascular plants, mammals, birds, reptiles, amphibians, ants, beetles, centipedes, cockroaches, crickets, scorpions and spiders). In the case of the belowground networks, our datasets included 95,208 Operational Taxonomic Units (OTUs) of bacteria, fungi, protists, and soil invertebrates. These OTUs (aka phylotypes) were calculated at 97%
sequence similarity and can be considered to be analogous to "species." However, because of the large number of microbial "species" compared with other groups (plants and animals) and the need to restrict analyses to a manageable network of interactions, we focused on the dominant microbial OTUs (top 10% species sorted by dominance, as described in Soliveres et al., 2016). Dominant species for bacteria, fungi, and other eukaryotes were obtained independently for these organisms from their original OTU tables. These bacterial, fungal, and other eukaryotic taxa were then merged into a single abundance table. This resulted in a dataset with 9,502 taxa including 4,953 bacteria (~80% of all bacterial phylotypes), 2,321 fungi (~80% of all fungal phylotypes), and 2,228 other eukaryotes phylotypes (~80% of all eukaryotic phylotypes). We then calculated all pairwise Spearman's rank correlations (ρ) between all soil plant/animal and soil microbe/animal taxa. We focused exclusively on positive correlations as they provide information on microbial taxa that may respond similar to environmental conditions (Barberán, Bates, Casamayor, & Fierer, 2012). We considered a co-occurrence to be robust if the Spearman's correlation coefficient ρ was > 0.50 and p < 0.01 (see Barberán et al., 2012 for a similar approach). The network was visualized with the interactive platform Gephi (Bastian, Heymann, & Jacomy, 2009). Finally, we used default parameters from the interactive platform Gephi to identify ecological clusters (aka modules) of soil taxa strongly interacting with each other (Bastian et al., 2009). We then computed the relative abundance of each ecological cluster by averaging the standardized relative abundances (z-score) of the taxa that belong to each ecological cluster. By standardizing our data, we ruled out any effect of merging data from different soil groups: plants/animals and soil microbes/animals. In addition, we also used an alternative approach and calculated the relative abundance of ecological clusters after centered log-ratio transformation. Information on functional traits for fungal taxa within each ecological cluster (which is unavailable for bacteria) was obtained from the online application FUNGuild described in Nguyen et al. (2016).

2.7 | Variation partitioning modeling

We used Variation Partitioning (Legendre, 2008) to quantify the relative importance of four groups of predictors: (1) six climatic legacies, (2) six climatic variables from current climate, (3) current management (cattle density in regional Australia and cattle density and cropping in continental Australia), and (4) soil properties (pH, % of sand, soil C and P) as predictors of the relative abundance of ecological clusters in the (1) aboveground network and (2) belowground network. This analysis allowed us to identify whether climatic legacies can explain a unique portion of the variance that is not explained by current climate or management (Legendre, 2008). Note that adjusted coefficients of determination (R²) in multiple regression and canonical analysis can, on occasion, take negative values (Legendre, 2008). Negative values in the variance explained for a group of predictors on a group of response variable are interpreted as zeros and correspond to cases in which the explanatory variables explain less variation than that explained using random normal variables (Legendre, 2008). In all cases, Variation Partitioning analyses were conducted with the R package Vegan (Oksanen et al., 2015).

2.8 | Random Forest modeling

We conducted a classification Random Forest analysis (Breiman, 2001) as described in Delgado-Baquerizo, Maestre, et al. (2016) to identify the major predictors of the relative abundance of ecological clusters in the two networks. Our list of predictors included six climatic legacies, six climatic variables from current climate, soil properties (pH, % of sand, soil C and P), and current management (cattle density and/or cropping). These analyses were conducted using the rPermute package (Archer, 2016) of the R statistical software (http://cran.r-project.org/). We also repeated these analyses using an alternative Random Forest approach using the gradientforest R package (Ellis, Smith, & Pitcher, 2012; Strobl, Boulesteix, Kneib, Augustin, & Zeilis, 2008).

2.9 | Structural equation modeling

We used structural equation modeling (SEM) (Grace, 2006) to evaluate effects of climatic legacies (i.e., temperature and precipitation differences between estimated climate about 20,000 ybp and current climatic estimates) on the relative abundance of ecological clusters in the two networks, after accounting for spatial autocorrelation (latitude and longitude), soil properties (pH, % of sand, soil C and P), current management (cattle density and/or cropping), and current climate. Our a priori model is shown in Supporting Information Figure S3. The use of SEM is particularly useful in large-scale correlative studies, as it allows the partitioning of causal influences among multiple variables and separation of the direct and indirect effects of model predictors (Grace, 2006). We then tested the goodness of fit of our models. The goodness of fit of SEM models was checked following Schermelleh-Engel, Moosbrugger, and Muller (2003). There is no single universally accepted test of overall goodness of fit for SEM, applicable in all situations regardless of sample size or data distribution (Schermelleh-Engel et al., 2003). We used the χ² test (χ²/DF; the model has a good fit when 0 ≤ χ²/DF ≤ 2 and 0.05 < p ≤ 1.00) and the root-mean-square error of approximation (RMSEA; the model has a good fit when RMSEA ≤ 0.05 and 0.10 < p ≤ 1.00) (Schermelleh-Engel et al., 2003). Our a priori models attained an acceptable/good fit by all criteria in all cases, and thus, no post hoc alterations were made. With a good model fit, we were free to interpret the path coefficients of the model and their associated p values. SEM models were conducted with the software AMOS 20 (IBM SPSS Inc, Chicago, IL, USA).

3 | RESULTS

We first generated two separate ecological networks for (1) aboveground and (2) belowground using information from the two
independent datasets. Using the approach described in the Methods section, we identified and calculated the relative abundance of six and seven major ecological clusters of species co-occurrence for aboveground and belowground networks, respectively (Figure 1). All taxa included within each ecological cluster for the two networks, and additional functional information on these taxa, are shown in Supporting Information Figures S4 and S5 and Table S1. These ecological clusters include multiple species linked by potential ecological interactions such as predator–prey, host–parasite, host–symbiont as well as different trophic levels, for example, primary producers and primary consumers (Supporting Information Table S1; Figures S4 and S5). We found a highly significant correlation between the relative abundance of the ecological clusters calculated as explained above and the same clusters calculated after using the centered log-ratio transformation ($q > 0.90; p < 0.001$; Supporting Information Table S2).

Our variation-partitioning model suggested that climatic legacies explained a unique portion of the variation for particular ecological clusters that could not be accounted for by the measures of current management, soil properties, or current climates (Figure 1). Climatic legacies explained a unique and significant portion of the variation of ecological clusters in five of six ecological clusters for our aboveground network (AG#) and for seven of seven ecological clusters for our belowground network (BG#) (Figure 1; Supporting Information Table S3). This was especially noticeable for AG#1 (6% of 58% of variation explained) and for BG#1 (7.5% of 68% of variation explained) and BG#3 (15.5% of 47% of variation explained). As expected, current climate and soil properties, routinely proposed as the dominant drivers of ecosystem community assembly at large-spatial scales, also explained a unique portion of the variation in all ecological clusters (Figure 1; Supporting Information Table S3). Management was also important for some clusters (BG#0, 1, 5 and 6), but not for others (Figure 1; Supporting Information Table S3).

Our Random Forest analyses suggested that climatic legacies were as important as, or more important than current climate in predicting the relative abundance of ecological clusters within our two networks and after accounting for soil properties and management (Supporting Information Figures S6–S9). Temperature legacies, maximum temperature (MAXT) and temperature seasonality (TSEA), were more consistent than precipitation legacies in predicting the relative abundance of ecological clusters within the aboveground and belowground networks (Supporting Information Figures S6–S9). However, mean precipitation (MAP) and precipitation seasonality (PSEA) were also reported to be a key climatic legacy predicting the relative abundance of ecological assemblies in both ecological networks (Supporting Information Figures S6–S9). These results suggest that climatic legacies have left a detectable signature on the contemporary ecosystem community assembly of unique clusters of plant, animal, and microbial species strongly co-occurring with each other (Supporting Information Table S1; Figures S4 and S5). Importantly, we found a statistically significant correlation between the Random Forest importances across predictors calculated from each ecological cluster using the rfPermute and gradientforest R packages (Supporting Information Table S4).

We used SEM, to further clarify the role of climatic legacies in predicting the relative abundance of contemporary ecosystem community assemblies, independently, for our two datasets. Although this is quite a conservative procedure, we still found multiple direct effects of climatic legacies, from all climatic variables studied, on the relative abundance of particular ecological clusters in both networks [Color figure can be viewed at wileyonlinelibrary.com]
Our findings provide novel evidence that past climates likely played an important role in regulating the relative abundance of the major ecosystem community assemblages that we observe today, helping to explain a unique portion of the variation in the distribution of particular communities that has generally been attributed to stochasticity (e.g., Powell et al., 2015). More specifically, climatic legacies might regulate the relative abundance of multiple ecological clusters formed by species strongly co-occurring within two independent above- and belowground networks (shown in Supporting Information Table S1). These co-occurring taxa included multiple potential ecological interactions such as predator–prey, host–parasite, host–symbiont, as well as different trophic levels, for example, primary producers and primary consumers (Supporting Information Table S1; Supporting Information Figures S3 and S4). For example, AG#1 contains multiple potential predator–prey interactions including (1) those of the birds species Struthidea cinerea and Turnix velox, with multiple potential plant and arthropod preys (Supporting Information Table S1), (2) those from the barking spider Selenocosmia stirlingi and the scorpion Lychas jonesae with the abundance of potential ant, beetle, and cricket prey, or (3) those from the lace monitor Varanus varius and the skink Ctenotus leonhardii, both of which are related to the abundance of a wide range of arthropod species that they prey on. Similarly, BG#1 contains potential predator–prey relationships such as the reported high correlation between the protozoan Cercozoa and Ciliophora and their common prey soil bacteria. This ecological cluster also contains multiple fungal plant pathogens such as Truncatella, Coniothyrium, and Phoma sp., with implications for plant communities co-existing with our belowground network. The relative abundance of all species and potential interactions within AG#1 and BG#1 might have been promoted by positive anomalies in maximum temperature (Figures 2 and 3). Supporting this result, BG#1 contains multiple phylotypes of bacteria that have previously been reported to respond positively to increases in temperature including those from the genera Candidatus, Koribacter, Bacillus, Burkholderia, and Rhodoplanes (Oliveiro, Bradford, & Fierer, 2016). In other words, locations with the highest positive anomalies in maximum temperature might now support a greater abundance of species within BG#1 than locations with negative anomalies or no changes in maximum temperature over the past 20,000 years.

Interestingly, increases in a given ecological cluster were often followed by declines in the relative abundance of other ecological clusters, as supported by the multiple indirect effects among the relative abundance of ecological clusters in our aboveground and microbe-animal networks. Such results suggest that increases in the relative abundance of particular ecological clusters resulting from temperature legacies might have had multiple cascading effects on other ecological clusters. Thus, the negative relationship between BG/AG#1 with BG/AG#2 might also lead to cascading effects on the relative abundance of BG/AG#3 clusters, which were negatively related to BG/AG#2 clusters in both networks (Figures 2 and 3). Thus, climatic legacies might also have multiple indirect negative or positive effects on the relative abundance of the ecological clusters within our two networks, as supported by our structural equation models (Figure 2). Cluster BG#2 in the microbe-animal network contained multiple probable mycorrhizal species such as Entoloma, Glomus, and Claroideoglomus, which might have positive effects on plant species linked to this soil microbial network; some identified using molecular techniques (Supporting Information Table S1). This ecological cluster also includes potential predator–prey relationships between soil amoeba and ciliates, with bacteria and plant pathogens (e.g., Gibberella intricans). Moreover, for the aboveground network, AG#2 was characterized by the potential producer–consumer link between emus Dromaius novaehollandiae and the fruits of Lycium ferocissimum, Eremophila debilis, and Einadia spp. (Noble, 1991). Our findings suggest that the relative abundance and potential interactions among species within all of these ecological clusters are highly sensitive to anomalies in maximum temperatures and their cascading effects (Figure 3). Changes in ecological clusters #2 in both networks, linked to climatic anomalies, might in turn have multiple cascading effects on the relative abundance of ecological clusters #3 in both networks. BG#2 is characterized by potential parasite–host interactions between Gregaria sp. and soil arthropods (Omoto & Cartwright, 2003), predator–prey interactions between phylotypes from phylum Cercozoa (protozoa) and bacteria (Supporting Information Table S1), and plant–fungal interactions of symbiosis (e.g., Auritella sp.) and pathogenesis (e.g., Devriesia sp.). Similarly, AG#3 is characterized by potential predator–prey interactions among plants, insects, lizards, and amphibians.

Although the effects of current or climatic legacies on the community assembly of terrestrial ecosystems are not directly comparable to those from ongoing changes in climate, our network approach still has the potential to provide insights into the role of climate change in predicting possible winner and loser community
FIGURE 2  Mechanistic modeling identifying the direct and indirect effects of climatic legacies on the relative abundance of ecological clusters within our aboveground and belowground networks. For simplicity, only effects with a $p < 0.01$ are reported here. The rest of significant effects are available in Supporting Information Table S5 ($0.01 < p < 0.05$). Numbers adjacent to arrows indicate the effect size. $R^2$ denotes the proportion of variance explained. The size of the arrow is proportional to the effect size (but in the case of spatial influence). Climatic legacies, current climate, and management predictors are included in our models as independent observable variables; however, we grouped them in the same box in the model for graphical simplicity. AG, aboveground network; BG, belowground network  [Color figure can be viewed at wileyonlinelibrary.com]
assemblies in response to climate change. Specifically, our study provides a compendium of species from particular ecological clusters that are expected to be highly sensitive to changes in climatic conditions. For example, current maximum temperature, one of the major climatic legacies, is also positively and strongly influencing the abundance of BG#1 (Figure 2) and AG#1 (SEM direct effect = 1.45; p = 0.044; Supporting Information Table S3). This suggests that further increases in temperature predicted by the end of this century might continue to promote the relative abundance of species and interactions within this ecological cluster, largely to the detriment of those in BG#2 and AG#2, with potential cascading effects on other ecological clusters. In fact, our findings suggest that positive anomalies of maximum temperature of up to 4°C—comparable to those predicted for climate change already had a massive effect on the relative abundance of particular ecological clusters (Figure 3). Predicted impacts of changes in precipitation with climate change (Huang, Yu, Guan, Wang, & Guo, 2016) could also be inferred from our network approach. For instance, for our aboveground network, current precipitation seasonality, whose legacy was positively related to the abundance of AG#4, indirectly via changes in soil pH, is still having an effect on the abundance of this ecological cluster, characterized for the potential interactions between the sand monitor (Varanus gouldii) and its prey items lycosid spiders (Lycosid spp.) and scorpions (Lychas spp.). Other examples, of key climatic legacies that still drive the relative abundance of particular ecological clusters can be inferred from Figure 2 and Supporting Information Table S1 and S3. These climatic changes could also alter the proportion of native species or the proportion of taxa coming from different species. For example, BG#1 in our microbe-animal network comprised mainly of phylotypes of strongly occurring bacteria and fungi, but BG#2 also contained multiple soil animal taxa.

Finally, as expected (e.g., Gossner et al., 2016), current management also influenced the relative abundance of ecosystem community assemblies. For example, for our belowground network, we found strong direct effects of cropping and cattle density on the relative abundance of the multiple ecological clusters within this network (Figure 2). Of special interest is the negative effect of cropping on the relative abundance of BG#1 in our microbe-animal network, which might potentially reverse part of the climatic legacies from maximum temperature (explained above) on this ecological cluster. Interestingly, BG#2 in the microbial-animal network, which was indirectly negatively affected by the maximum temperature legacy, seems to benefit from cropping and cattle density impacts (Figure 2), though indirectly, potentially helping to reverse climatic legacies on BG#1. All of these results accord with previous studies suggesting that human activities can erase part of the climatic legacies of temperature and precipitation on the current distribution of soil organisms (Delgado-Baquerizo et al., 2017). However, in general, management measured as cattle density did not influence the relative abundance of aboveground clusters as supported by our Variation Partitioning, Random Forest and Structural Equation Modeling.
analyses. The only ecological cluster affected by cattle density in this network was AG#5, shown in our Random Forest results (Supporting Information Figure S6).

Together, our work suggests that climatic legacies have left a statistically significant signature on the contemporary below- and aboveground community assemblies and can now explain a unique portion of the distribution in particular ecological clusters from terrestrial ecosystems. This is true even after accounting for key predictors, such as location, soil properties, current climate, or management, all of which are routinely proposed as drivers of ecosystem community assemblies at large spatial scales. These findings also advance our understanding of the links between particular climatic legacies and the relative abundance of species and potential interaction within ecological clusters across a broad range of ecosystem types at the continental scale. Moreover, we found that climatic anomalies might have led to multiple cascading effects on the relative abundance of ecological clusters in terrestrial ecosystems. We also found that current management influences can potentially reverse part of the impacts of climatic legacies, which occurred during the last 20,000 years, on particular ecological clusters. Such knowledge can potentially help us to better understand changes in particular ecosystem community assemblies in response to ongoing global environmental change including land use intensification and climate change, with important implications for future sustainable management and conservation policies.

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AUTHOR CONTRIBUTION

M.D-B. conceived this study. The aboveground dataset was compiled by D.J.E., S.K.T., J.V., and I.O. The belowground dataset was compiled by A.B. M.D-B. conducted network and statistical modeling. The manuscript was written by M.D-B, edited by D.J.E., and all co-authors significantly contributed to improve it.

DATA ACCESSIBILITY

Data associated with this paper has been deposited in figshare: https://figshare.com/s/899e610ba9fd353cae49 (10.6084/m9.figshare.621754). The raw sequence data used in this study is available at https://data.bioplatforms.com/organization/about/australian-microbiome.

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