Variation and adaptation of leaf water content among species, communities, and biomes

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Abstract
Leaf water content (LWC) is essential for the physiological activities in plants, but its spatial variation and the underlying mechanisms in natural plant communities are unclear. In this study, we measured the LWC of 5641 plant species from 72 natural communities in China, covering most terrestrial ecosystems, to answer these questions. Our results showed that LWC, on average, was 0.690 g g\textsuperscript{-1}, and was significantly higher in forests and deserts than in grasslands. LWC was significantly different among different plant life forms, and ranked on averages in the following order: herbs > shrubs > trees. Interestingly, LWC decreased with increasing humidity and increased in dry environments. Furthermore, the variations of LWC in plant communities were higher in arid areas and those species with lower LWC in a plant community were more sensitive to changing environments. These results demonstrated the adaptations of plants to water regime in their habitats. Although, phylogeny has no significant effect on LWC, plant species both in forests and grasslands evolve toward higher LWC. Variations of LWC from species to community to biome represent the cost-effective strategy of plants, where plant species in drier environment require higher input to keep higher LWC to balance water availability and heat regulation. This systematic investigation fills the gaps on how LWC varies spatially and clarifies the different adaptation mechanisms regulating LWC across scales.

1. Introduction
Leaves, as hubs between soil and atmosphere, are one of the most important organs of plants and the main drivers of energy flow and element cycles in terrestrial ecosystems (Chapin \textit{et al} 2011). Most physiological activities involved in transpiration and photosynthesis in leaves are impossible without the participation of water (Chapin \textit{et al} 2011) (figure S1 available online at stacks.iop.org/ERL/16/124038/mmedia). During photosynthesis and respiration, water is not only a participant and product, but also an important solvent (Kromer 1995, Hohmann-Marriott and Blankenship 2011, Bernacchi and VanLoocke 2015). Transpiration tension caused by vapor pressure difference (VPD) is directly related to the water content of the leaf epidermis and absorption of root nutrients (Boyer 1985). Commonly, under water deficiency, plants can maintain the water status of living leaves and ensure normal physiological functions at the expense of falling old leaves and ensure normal physiological functions at the expense of falling old leaves to reducing the water demand (Gutschick and BassiriRad 2003). A stable water status in living leaves is essential for plant survival.

However, previous research on leaf water content (LWC) focused on the species level mostly in agricultural ecosystems for monitoring crop growth (Pan \textit{et al} 2019), and did not fully consider its physiological and ecological importance, and did not fully consider its physiological and ecological importance. Although LWC is estimated in communities to improve the
radiative transfer models that could simulate light penetration and scattering (Zhu et al 2017), there has been no direct study on LWC at a large scale. Thus, the LWC in different natural communities (e.g., different vegetation types and functional groups) remains unclear. We also do not understand how changing environments and plant evolution affect LWC in particular. Exploring LWC at a large scale can help to further our understanding of the responses and the adaptation of plants to the changing environment.

Plants are known to develop strategies to adapt to or defend against environmental challenges (Grime 1977, Hooper et al 2005, Reich 2014). Plants will adjust their traits to optimize the utilization of resources and maintain optimal productivity. Thus, when a resource is scarce, the ability of traits associated with accessing that resource increases. Therefore, plant leaves may tend to more water to maintain normal physiological functions and survive under extreme conditions. Researchers have found that succulents with higher LWC are the most persistent xerophytes resisting extreme arid conditions (Grime 1977). Based on these results, we assumed that intra-community variation (i.e., variation across all species within a community) was driven by environmental factors. However, how the environmental gradients affect the intra-community variation remains unclear.

Previous studies of plant traits have explored the spatial variations in living leaves across species, communities, and regions (Liu et al 2017, Li et al 2018, Zhao et al 2019, Zhang et al 2020). However, there have been no studies on LWC at different scales. To investigate the applicability of the theory of optimal trait evolution (traits adapt to the changing environment to maximize their growth rate and optimize resource use) (Norberg et al 2001, Liu et al 2020) and trait drive theory (Enquist et al 2015, Lourenço et al 2020) in communities systematic information on how plant traits vary at different scales is necessary to explore the responses and adaptations of plants in natural communities to altering environments.

Leaves of different species have different LWC. Understanding the variation in LWC among species in a community is helpful to understand the adaptation characteristics of plants to the environment and the filtering effect of the environment on plants. Owing to the lack research of LWC at the biome scale, how the variation in LWC within a community responds to changing environment remains unclear. Therefore, indexes of variance are needed to explore the relationships between the variation in LWC and environmental gradients. In addition to the commonly used variance, the coefficient of variation (CV), Gini coefficient, and entropy of LWC could also describe such variation from multiple perspectives (Sala-I-Martin 2002). Unfortunately, few studies have used these indexes to describe the variation in LWC due to a lack of matched and systematic data (i.e., plant traits associated with corresponding species and community) in natural communities (Tian et al 2016, Wang et al 2016, Li et al 2018, He et al 2019), even in the well-known trait database of TRY (www.try-db.org) (Correspondence, Kattge et al 2020). Furthermore, such large-scale field investigations are time-consuming and expensive.

China is an ecologically diverse country, containing many types of plant communities and thus providing an ideal place for conducting a natural experiment to explore the responses and adaptations of plant traits to changing environments across many biomes. In this study, we used standardized, consistent measurement procedures to collect the LWC data of living leaves from 5641 plant species belonging to 72 natural communities of China. Our aim was to explore the variation and adaptation mechanisms of LWC from different species, communities, and biomes. The main objective of this study was to provide suitable answers to the following questions: (a) What is the average LWC of different natural communities? (b) How does LWC vary across species, communities, and biomes, and what are the underlying mechanisms of this variation?

2. Materials and methods

2.1. Study site

In a combination of representative vegetation communities across many spatially even conditions, we set up a total of 72 field investigation sites (figure 1), which covered most the plant communities in the Northern Hemisphere. These plant communities included forest (deciduous needle-leaf forest, evergreen coniferous forest, deciduous broadleaved forest and broad-leaf evergreen forest), grassland (meadow, typical and desert grasslands), and desert (Li et al 2018). To avoid anthropogenic disturbance as much as possible, the communities investigations were located in national reserves or long-term monitoring plots of ecological field stations.

For these sites, the mean annual temperature (MAT) is in the range of 6.8 °C–23.2 °C and mean annual precipitation (MAP) ranges from 25.0 to 2265.8 mm. The areas straddle several climatic zones in the Northern Hemisphere from north to south, including boreal forests, temperate seasonal forests, broad-leaved forests, subtropical evergreen broad-leaved forests, tropical seasonal rain forests, and rain forests. From east to west, the climate shifts from humid to arid, and the vegetation include forest, grassland and desert (figure 1). Climate data were derived from the interpolation of records from meteorological stations across China during 1961–2010, and the humidity index (HI) data were obtained from CGIAR-CSI database 1970–2000 (here, HI = Rainfall/Potential Evapotranspiration).
2.2. Field sampling

To ensure the homogeneity of measured data, field investigations were carried out in the periods of peaks growth of plant communities from June to August in 2013–2019. In contrast to typical methods used in plot investigations (Zhao et al. 2019), a recently developed method for the collection of data from all species in the sampling sites was adopted (Zhang et al. 2020). The typical method represents a quadrat survey focusing on the dominant species. In practice, traits of all visible plant species within 1 km around the sample site were collected to obtain more comprehensive data. For all species, we only sampled the unshaded, fresh and complete leaves, and we selected 20–30 leaves from more than four individuals to represent each species. Samples of living leaves were kept in plastic bags and stored in ice boxes. Samples from a total of 5641 plant species were collected, representing 30 forest ecosystems, 25 grassland ecosystems and 17 desert ecosystems. The highest number (306 species) of plant species was sampled in Xishuangbanna in Yunnan, and the lowest number (6 species) was sampled in Qiemo in Xinjiang.

LWC was measured within 2 h after the samples were collected in order to reduce errors. First, the fresh weight (FW) of no fewer than 10 leaf samples was determined using an analytical balance; then leaves were transferred to an oven set at a temperature at 70 °C for 48 h to ensure they achieved constant weight. Lastly, the dry weight (DW) was measured. LWC (g g⁻¹) was calculated using the following equation (Garnier and Laurent 1994):

\[ \text{LWC} = \frac{\text{FW} - \text{DW}}{\text{FW}}. \]  

Dominant species in communities were identified by the importance value from the data of plant community composition (Lamont et al. 1977, Zhang et al. 2015). Plant community structures of the 72 sites were investigated using the quadrat method (Wang et al. 2015, Li et al. 2018) (figure S2). Tree, shrub, and herb quadrats were set at the same time to ensure matching and systematization of data. Forest community included tree, shrub and herb quadrats. Grassland community included herb quadrats. Desert community included shrub and herb quadrats. Dominant species of the forest were confirmed by the order of relative biomass. The biomass of each species in the quadrats (30 m × 40 m) was calculated using plant biomass equations. The biomass of dominant species should account for more than 10% of the total biomass. Dominant species of grasslands and deserts were confirmed by using relatively important values of frequency, quantity, and coverage. The relative frequency, relative quantity, and relative coverage of species in eight quadrats (1 m × 1 m) were calculated (Zhang et al. 2020). The important values of dominant species had to be greater than 10%. The dominant species in desert was confirmed by the order of relative biomass and important values, which was calculated using plant biomass equations in the larger quadrats (10 m × 10 m), and was calculated using the important value reference from the grasslands in the herb quadrats (1 m × 1 m). Plants are classified into three plant functional groups: tree, shrub and herb, across communities.

2.3. Calculation of the phylogenetic signal K-value

To explore the effect of genetic evolution on the spatial variation of LWC, we constructed phylogenetic
trees and calculated phylogenetic signals. After calibrating the family, genus, and species names of each species on the basis of www.theplantlist.org, we used ‘S.PhyloMaker’ software to construct phylogenetic trees (Qian and Jin 2015), and the phylogenetic signal, K-value (Blomberg’s K value) (Blomberg et al 2003), was calculated using the ‘Picante’ package in R (version 3.6.3; R Development Core Team, Vienna, Austria) (Zhang et al 2020). We then calculated the phylogenetic signal intensity of each species in families that had more than ten species. In the analysis of the relationship between LWC and evolution, the family divergence time was defined by the earliest diverging genus in a family (Ma et al 2018).

2.4. Calculation of inequality indices
For estimating the variation of LWC in natural plant communities, four classic inequality indices were used. These indices were variance, CV, Gini coefficient, and entropy, known as discrete coefficients (Benettin et al 1976, Sala-I-Martin 2002, Castellanos et al 2016). The indices were normalized between 0 and 1 (Castellanos et al 2016). The inequality indices were calculated using the ‘Performance Analytics package’ in R.

2.5. Data processing
The data of LWC are represented as the mean value and 95% confidence interval. We use one-way ANOVA to test the significance of factors and Tukey HSD to compare data between different communities. Quadratic regression analysis (with lower AIC (Akaike information criterion) compared to linear regression) was used to explore the simple relationships between LWC and MAT, MAP and HI by SigmaPlot 10.0 (Systat Software, Point Richmond, CA, www.systatsoftware.com), and the relationship between divergence time and LWC (weighted by the number of species). The quantile linear regression was used to explore the variation in LWC within communities using the ‘quantreg’ package in R. The distribution of sampling plots was built using ArcGIS 10.1 (Version 10.1; Redlands, CA, USA). Density graphs of LWC were created using R (version 3.6.3; R Development Core Team, Vienna, Austria, 2012, www.R-project.org). SPSS 13.0 (Chicago, IBM Corp, USA) was used for statistical analyses of data (P < 0.05).

3. Results

3.1. Changes in LWC
The average LWC of 5641 plant species was approximately 0.690 ± 0.002 g g\(^{-1}\). The average LWC of plants from deserts and forests was higher than that of grasslands to some extent and the order was as follows: desert (0.699 g g\(^{-1}\) > forest (0.696 g g\(^{-1}\)) > grassland (0.667 g g\(^{-1}\)) (figure 2, table S1). Furthermore, LWC differed significantly among different plant functional groups and the order was as follows: herb (0.736 g g\(^{-1}\)) > shrub (0.665 g g\(^{-1}\)) > tree (0.615 g g\(^{-1}\)). The LWC of herbs in different communities was significantly higher than that of trees and shrubs (tables S1–S5), and the LWC of herbs in forests was significantly higher than that in grasslands and deserts (table S2). Different forest communities differed significantly in LWC, with the highest in evergreen coniferous forests (0.704 g g\(^{-1}\)), and the lowest in broad-leaved evergreen forests (0.678 g g\(^{-1}\)) (table S3).
3.2. Variation of LWC in natural plant community in different environmental conditions

There was a significant linear correlation between LWC and MAP ($R^2 = 0.21^{**}$), and between LWC and HI ($R^2 = 0.23^{***}$) (figure 3). LWC first decreased and then increased with increasing MAP and HI. According to our results, LWC was higher in arid and humid environments. Furthermore, there were significant differences in the coefficients of linear equations from the analysis of different quantiles (5th, 25th, 50th, 75th, and 95th), and the linear fitting of these quantiles differed with different environmental factors (figure 4). The fitting equations for different quantiles of LWC and environmental factors showed significance differences ($P < 0.05$) (table S6). The selected inequality indices were significantly negatively correlated with precipitation and humidity, especially for variance ($-0.45$) and CV ($-0.38$) (table 1). In arid environments, the LWC of plant communities were more prone to greater inequality. The inequality indices showed a strong correlation with the lower boundary of LWC (below the 5th quantile at the community level) and the correlation coefficient was 0.8 ($P < 0.001$) (table 1).

3.3. Evolutionary trends of LWC in natural communities at large scale

The LWC of plant species in different communities increased significantly with the progress of evolution, except for desert species (figure 5). Significant phylogenetic signals of LWC were observed in different communities and different plant functional groups (figure 6, S3). However, Blomberg's K values for all were very weak, and LWC was therefore not considered to be strongly constrained by phylogeny (figure 6).

4. Discussion

4.1. Changes in LWC in different vegetation types and life forms

LWC ranged from 0.06 to 0.99 g g$^{-1}$ with a mean of 0.690 g g$^{-1}$ at the biome scale. To the best of our knowledge, this was the first study to explore the variation in LWC in a consistently measured database. Thus, it was difficult for us to compare our results with those from other studies, except for the results at local scales or on specific species. We clearly demonstrated that the LWC of plant species of different life forms were significantly different. The LWC of trees was lower than that of herbs, which was consistent among different vegetation types (tables S1–S5). This finding probably reflects the fact that tree species are mostly perennial plants in forest communities with longer growth periods and slower growth rates (Grime 1977, Garnier and Laurent 1994). However, most herbs have a lifespan of less than a year with short growth periods and fast growth rates, and can therefore complete their life cycle in a short time (Grime 1977, Coley et al 1985, Coley 1988). Therefore, the significant differences in LWC between different plant functional groups (high in herbs and low in trees) is an adaptation of plants to the environment. It was unexpected that LWC of herbs in forests was higher than that of herbs in other communities (grassland and desert) due to the shading effect that created, a wet and humid environment (Grime 1977). Through the large-scale quantification of LWC, we obtained the LWC of different vegetation types and different functional groups, which provides a new reference for the study of natural communities. However, the differences between different types of forests need to be further explored in the future.

4.2. Spatial variation in LWC and the effect of humidity

The average of LWC in communities decreased significantly with increasing precipitation and humidity indices at the biome scale (figure 3). Water, as an essential factor for the survival of plants, is a higher...
Figure 4. Quantile linear regression coefficient test (5%, 25%, 50%, 75%, 95%) for the variation of leaf water content within communities. The equation is $y = ax + b$. The upper part of the figures (a)–(c) shows the value of coefficient $b$ at five different sub-points, and the figures below showed the value of coefficient $a$ at five different quantiles. The red solid line represents the average coefficient. MAP, mean annual precipitation; MAT, mean annual temperature; HI, humidity index.

Table 1. Correlation coefficients between the quantiles of leaf water content (LWC) in community and environmental factors.

| Type                        | Variance | Coefficient of variance | Gini coefficient | Entropy |
|-----------------------------|----------|--------------------------|------------------|---------|
| Environmental factors       |          |                          |                  |         |
| MAP (mm)                    | −0.41*** | −0.34**                  | −0.23*           | −0.32** |
| MAT (°C)                    | −0.04    | −0.01                    | −0.00            | −0.01   |
| HI                          | −0.45*** | −0.38***                 | −0.29*           | −0.35** |
| Boundaries of LWC in community |        |                          |                  |         |
| Lower (quantile at 5th)     | −0.76*** | −0.80***                 | −0.77***         | −0.75***|
| Upper (quantile at 95th)    | 0.21***  | 0.14*                    | 0.15**           | 0.15**  |

* MAP: mean annual precipitation; MAT: mean annual temperature; HI: humidity index.

b Level of significance: ***: $P < 0.001$; **: $0.001 < P < 0.01$; *: $0.01 < P < 0.05$.

requirement in arid environments. Plants growing in an environment where water availability is restricted, gain the chance to survive at the expense of ‘minor profits,’ which is a trade-off commonly known as an ecological strategy (Hetherington and Woodward 2003, Liu et al 2017). Species can deal with some harsh environments by increasing their water content, especially in leaves, as they are a vital organ for survival and development (Grime 1977, Gutschick and BassiriRad 2003). The evolutionary history of LWC reflects active responses and positive adjustments during plant growth and development across various phylogenies. It is interesting to note that forests and grasslands have evolved toward higher LWC; however, weak phylogenetic signals indicate that plants are mainly affected by the environment rather than by evolutionary adaptations. It should be noted that the impact of phylogeny may be different for different leaf stages (young, mature or senescent). However, we focused on evolutionary influence on mature leaves in this study. Whether the impacts of phylogeny on LWC vary with leaf stages is interesting and merit further investigation. Commonly, plants would maintain relatively stable LWC to maintain their physiological functions. Water in living leaves is one of most important factors for effectively regulating many physiological processes. The relationship between specific leaf area (SLA), VPD, and LWC provides conclusive evidence of the maintenance of leaf water status during stress (Nautiyal et al 2002). Researchers have recognized that LWC closely depends on leaf morphology and anatomy that is associated with photosynthetic activity (Wilson and Cooper 1967, Garnier and Laurent 1994). Therefore, plant species with a stable water content in their living leaves can survive and develop in the complex environment for a long time (Grime 1977). In other words, the stability of plant physiological processes and the relative stability of LWC are manifestations of long-term adaptations of plants to the environment. Under extreme drought, plant species can survive by excising the large number of leaves until they have the chance to regain their vitality (Gutschick and BassiriRad 2003).

4.3. Lower intra-community variation in LWC with increasing humidity

Extreme environments usually have more specific requirements for plant traits (Brotherton and Joyce 2015). As expected, significant correlations between inequality indices of LWC and environmental gradients existed, which justified that intra-community variation in LWC was driven by environmental factors as discussed in the introduction (table 1). If combinations of plant functional traits occur repeatedly in distantly related groups over a wide geographical
Changes to the leaf water content (LWC) among different communities over divergence time at the family level. LWC: leaf water content; R: correlation coefficient. ****: P < 0.001; ***: 0.001 ≤ P < 0.01; *: 0.01 ≤ P < 0.05. The divergence time of the earliest genus in a family was defined as the divergence time of the family. Bubble size represented the number of species used in (a)–(c). The larger circle indicates that more species were included in the family.

Figure 5. Changes to the leaf water content (LWC) among different communities over divergence time at the family level. LWC: leaf water content; R: correlation coefficient. ****: P < 0.001; ***: 0.001 ≤ P < 0.01; *: 0.01 ≤ P < 0.05. The divergence time of the earliest genus in a family was defined as the divergence time of the family. Bubble size represented the number of species used in (a)–(c). The larger circle indicates that more species were included in the family.

4.4. Variation in LWC at multiple scales jointly reflects the adaptation of plant species

Variation in LWC at the species, community, and biome scales can jointly reflect the adaptation strategies of plant species to changing humidity to some extent (figure 3). LWC is affected by humidity, which is important for determining the distribution of LWC not only at the species level, but also at the community level. Furthermore, there were larger variations in LWC in these water-limited communities (table 1). These findings verified our assumption that plant species, under the conditions of extreme drought, may adopt one of two divergent ecological strategies to survive in extreme environments, resulting in greater inequality in LWC, which we found was higher in drier environments (tables 1, S6–S9). In short, LWC exhibits two different ecological strategies in arid communities; one is the higher community LWC (table S1, figure 3), and the other is the greater inequality within the community (table 1).

Our results illustrated that drought may elevate the intra-community variation and average LWC, which was the response of plant species to increasing drought from another perspective. Global climate change is projected to increase the frequency and duration of droughts as temperatures increase (Dai 2011). Recently, warmer weather and droughts have occurred more frequently, which have had detrimental effects on ecosystem productivity (Webb et al 1983, Choat et al 2012). Research has previously shown that increasing CO₂ concentrations reduce the rate of water loss and carbon gain and increase the water use efficiency of terrestrial ecosystems (Breshears et al 2005, Ponce Campos et al 2013). Particular traits of plant species show significant patterns with climate, although the effect of climate on species relationships are modest (Wright et al 2004, Liu et al 2017). Therefore, plant species should evolve towards higher LWC in natural plant communities under the scenario of global climate change.
Figure 6. Phylogenetic tree and phylogenetic signal $K$-value of 5546 plant species in China. $K$-value (Blomberg's K value) indicates the phylogenetic signal for the leaf water content. $^{\ast\ast\ast}: P < 0.001; ^{\ast\ast}: 0.001 \leq P < 0.01; ^{\ast}: 0.01 \leq P < 0.05.$

Figure 7. Variation and adaptation mechanisms of leaf water content (LWC) under changing environment at large scales. Plants in humid environments have no requirement to keep high LWC by developing diversified physiological and ecological approaches. In contrast, plants in arid environment generally have higher LWC. At the community level, it has greater internal variation and more energy investment in humid environments to obtain limited water resources. These variations of LWC within communities and across larger spaces jointly form the adaptation mechanism of plants to balance the investment and gain in different environments.
(Grime 1977) to maintain the relatively stable LWC for maintaining normal photosynthesis function; (b) low-input opportunity, where plant species have high and low LWC; only when resources are very low, they bear the costs of lowering all activities related to photosynthesis (Hohmann-Marriott and Blankenship 2011). Of course, natural plant communities use a combination of strategies; some intermediate types that regulate LWC to adapt to altered environments can be found. As with other leaf traits in the spectrum of leaf economic types, these ecological strategies are the result of trade-offs between resource acquisition and survival for plant species in the long run (Wright et al 2007, Kong et al 2014, Reich 2014).

Based on the data of 5641 plant species in China (figure 4, table S6), we found that the variation range of LWC in plant communities was adjusted to adapt to changing environments, and the underlying ecological strategies were different for extreme (drought) and more suitable environments (wetness). In detail, from the perspective of spatial variation, the average value of LWC was relatively higher in drier or wetter climates, but the lowest in moderate climates (figure 7). Maintaining high water content is a crucial strategy for drought tolerance (Ravindra et al 1990, Nautiyal et al 2002). In specific communities, the variation in LWC for different plant species increase with increasing drought. The survival rules of dry environments are clearer, in which different plant species use different strategies to keep LWC stable, resulting in a wider water-use niche (Grime 1977). In contrast, plant species in humid climates do not require diversified physiological and ecological approaches to obtain optimal water in living leaves, which results in a narrower range of LWC in such communities. It was noted that the evolution of LWC in plant communities evolved towards higher values over longer time scales to some extent (figure 7). We speculated that for plant species, being able to acquire and store water may require higher energy inputs as an investment process because water is essential yet limited for plants in dry environments (Bernacchi and VanLoocke 2015). As a whole, plant communities will have greater internal variation (higher inequality) in drier scenarios and vice versa, because in wetter environments, water is no longer a limited resource and plant species do not need to invest more energy to obtain it.

5. Conclusions

LWC shows a normal distribution with a mean of 0.690 g g$^{-1}$ in China. LWC of forests and deserts was significantly higher than that of grasslands and was also different among different plant functional groups. Our findings provide the first evidence that humidity is the main factor in determining the spatial distributions of LWC at the biome scale. Drier environments had higher average values of LWC and higher interspecific variation. Communities may evolve toward higher LWC due to the droughts caused by global warming, although weak phylogenetic signals of LWC are observed. The change in LWC with humidity, both at the community and local levels, could reflect the results of different ecological strategies of plant species to balance energy input and gain. Plant communities have larger inequalities in interspecific variation and higher energy investment in arid areas, while the reverse is true in humid environments. Variations within a community and across large spaces represent the adaptation mechanism of plants to balance investment and gain at different scales. Our findings provide new insights and a basis for exploring the relationship between plants and the environment.

Data availability statement

The data used to support the findings of this study are available from the corresponding author upon request. You can download the dataset files using the url below: https://datadryad.org/stash/share/ehUb8QQQaa5ItnGatfs8mtvVploLoLo1an1pckfbck

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Author contribution

R W and N H conceived the ideas and designed methodology; R W, L X, M L and N H collected the data; R W and N H analyzed the data; R W, N H and S L led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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