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Climatic hydration conditions and biome specific carrying capacity define patterns of common and rare soil bacterial distributions

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Soil bacterial richness is affected by climate, vegetation and soil type

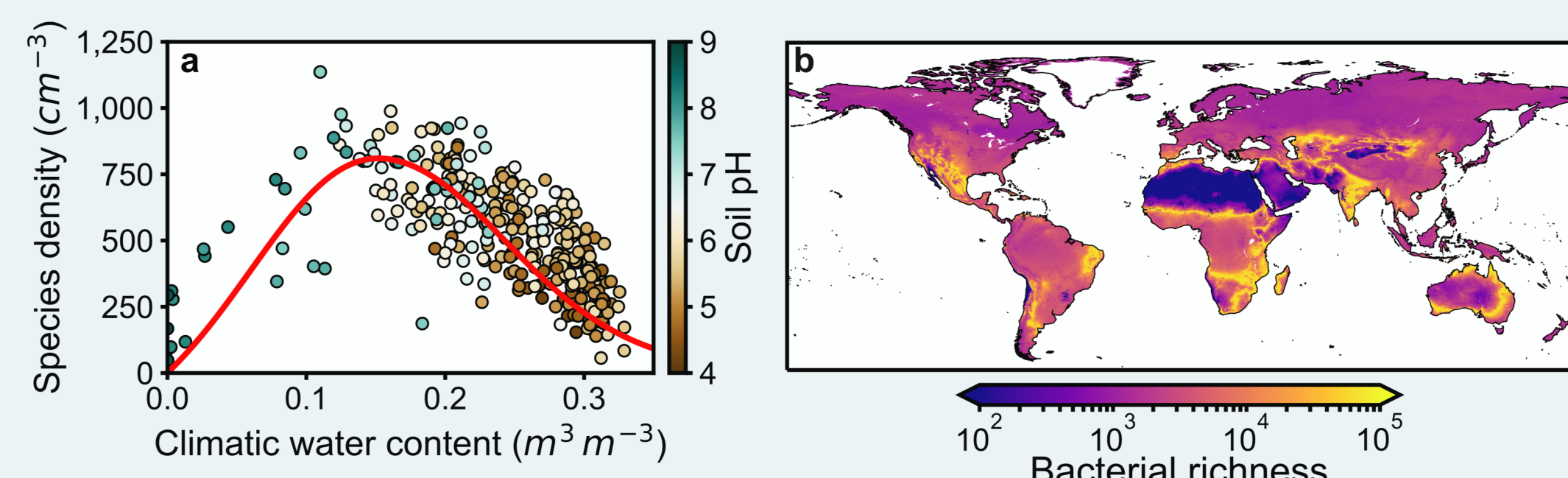


Fig. 1: Soil bacterial richness is mediated by carrying capacity and aqueous phase connectedness. **a.** Species density of recent bacterial diversity data^{1,2,3} is well described using an aqueous-phase fragmentation-based heuristic model (HM, red line). **b.** Global map of modeled bacterial richness predicted with the HM. High values of richness occur in the climatic transition zones (e.g. Sahel).

- Soil bacterial **carrying capacity** can be related to **net primary productivity (NPP)** and **mean annual temperature (MAT)**
- Bacterial **richness is attributed to aqueous (micro-) habitat fragmentation** by a heuristic model and peaks at intermediate climatic water contents (CWC): $Richness = f(CWC, NPP, MAT, soil\ type)$ (Bickel and Or, *accepted*)
- Often quoted relations of bacterial richness with **soil pH** are explained by **climatic water balance** (Slessarev *et al.*, 2016)
- **Diversity is better explained** by environmental variables when **more weight is given to rare species** (Bickel *et al.*, 2019)

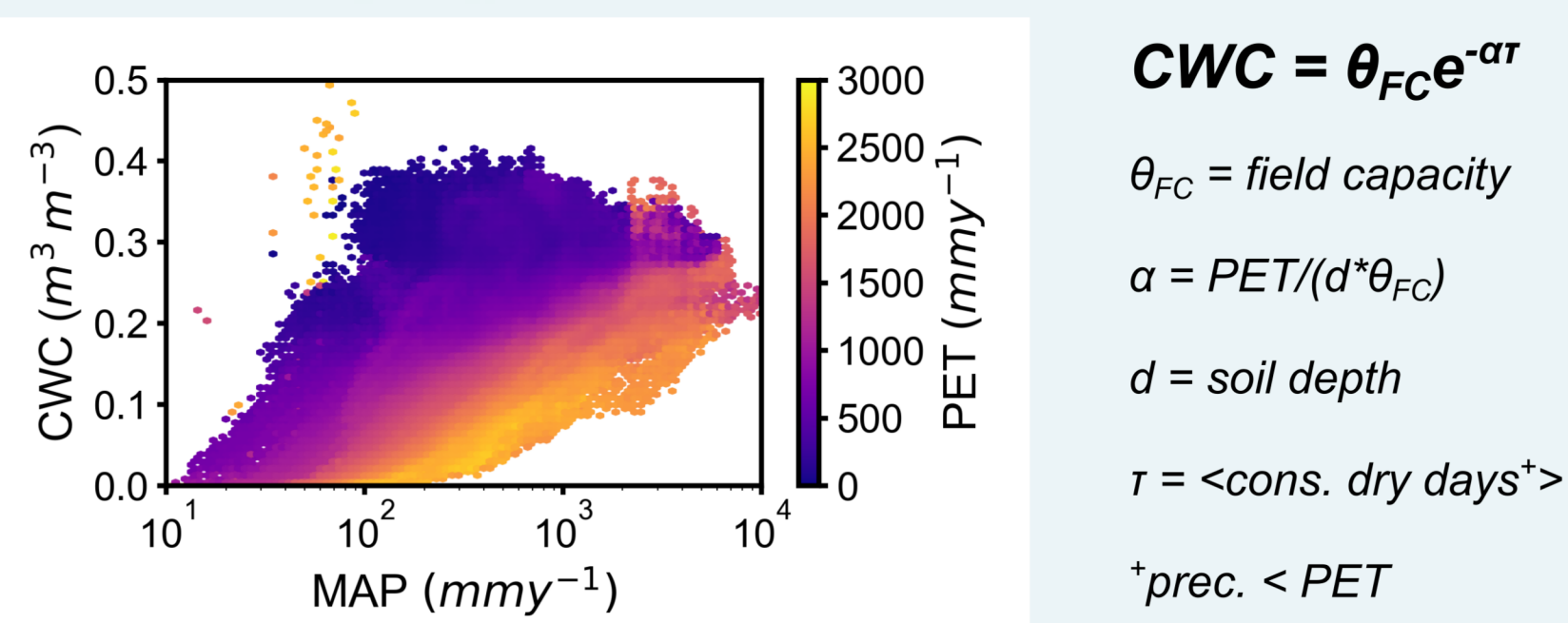
>>> How are common and rare bacterial species globally distributed in soils of different biomes?

Objectives are to:

- classify rare and common species based on prevalence and,**
- model their distinct sensitivities to environmental factors** (water content, carrying capacity)

Diversity meta-analysis across biomes

Climatic soil water contents (CWC) based on rainfall frequency, potential evapotranspiration (PET) and water holding capacity



Spatially-explicit individual-based model (SIM) of diverse bacterial communities

- heterogeneous soil surface with water film thickness prescribed by water content
- Individual cells grow on three identical, diffusible carbon sources
- Passive (shoving) and active (swimming) motility where sufficiently wet
- Species are represented by permutations of growth rate and affinity per nutrient
- The detailed, computation-heavy SIM confirms trends of richness and carrying capacity as predicted by the simpler heuristic model (HM)

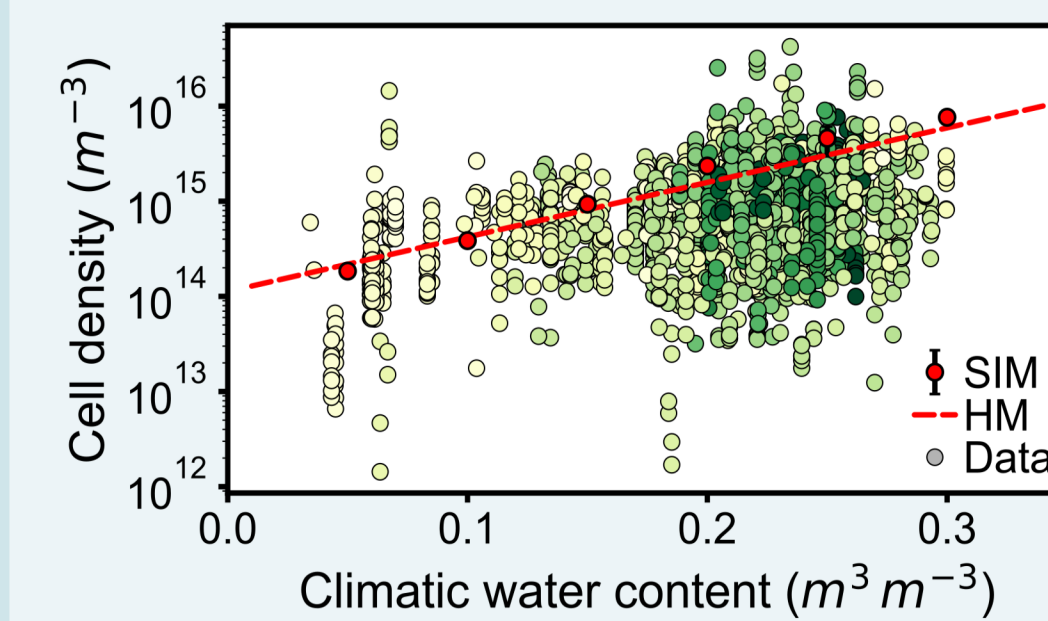


Fig. 2: Carrying capacity increases with climatic water content. Estimates of cell density from soil microbial carbon data⁴ colored by NPP. Simulation results from the SIM with prescribed carrying capacity ($2 \times 10^{17} m^{-3}$). An upper bound on cell density given by the heuristic model (HM).

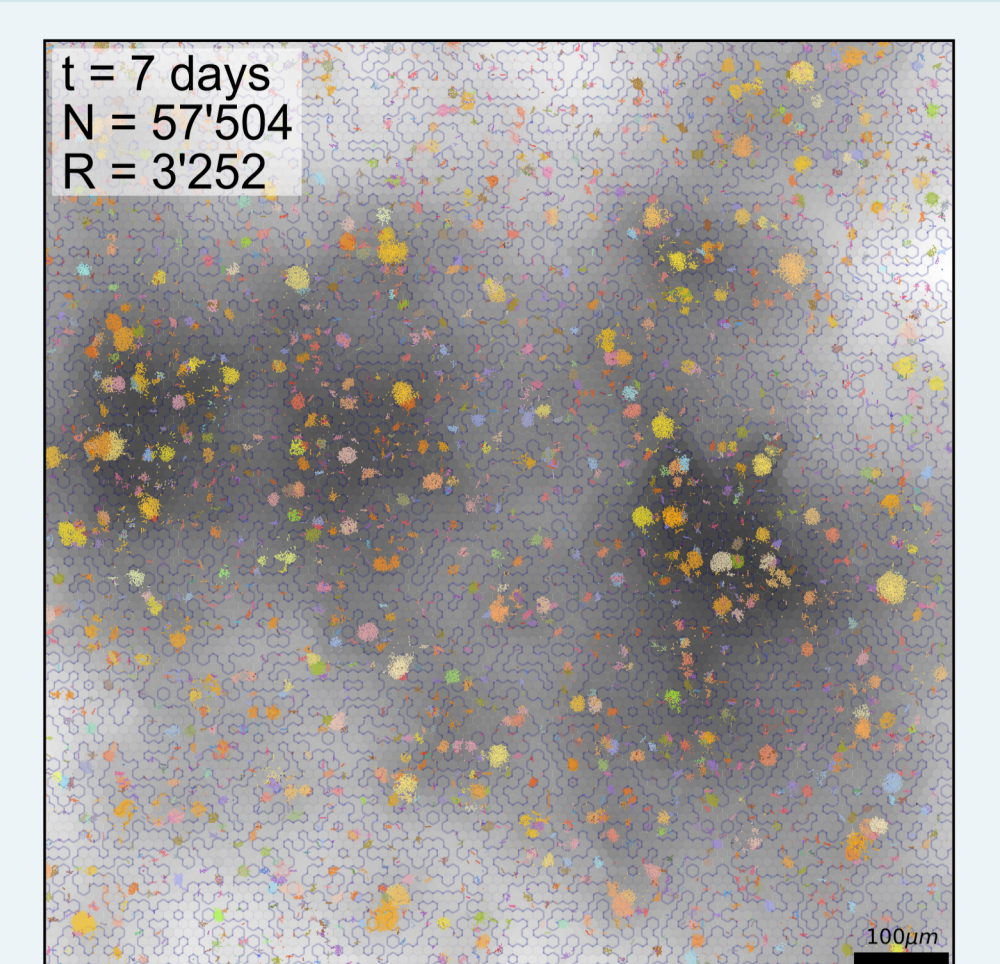
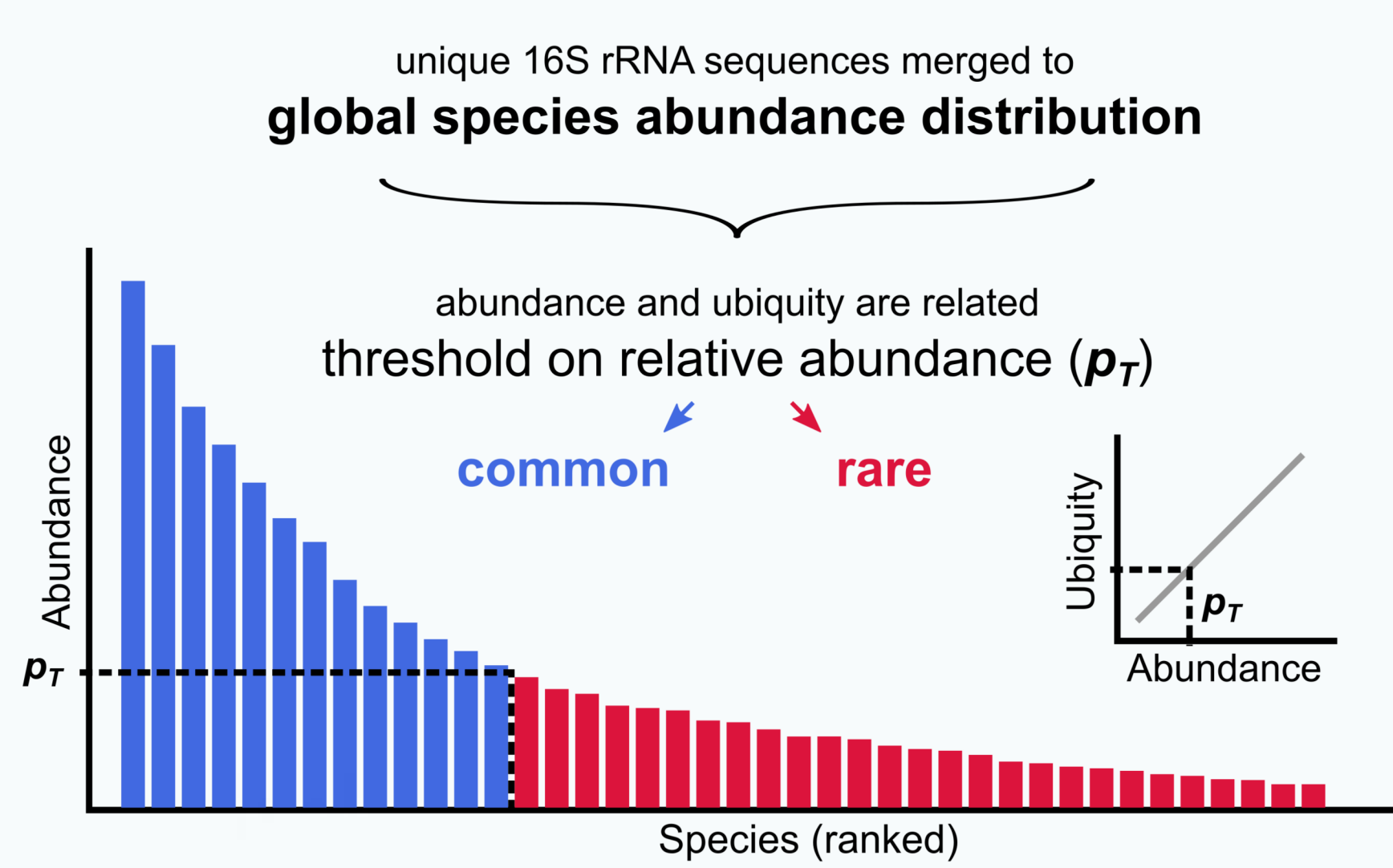
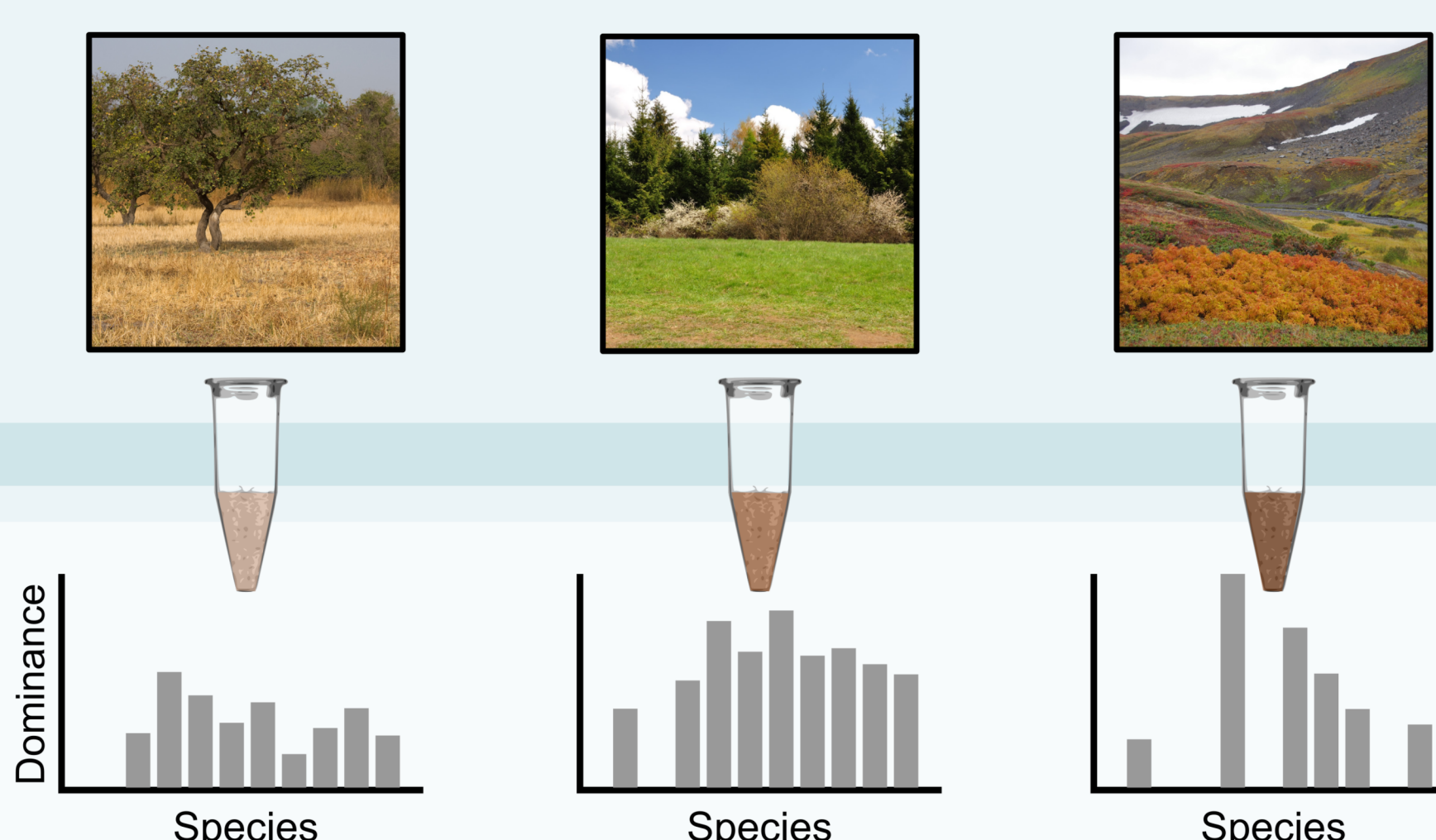
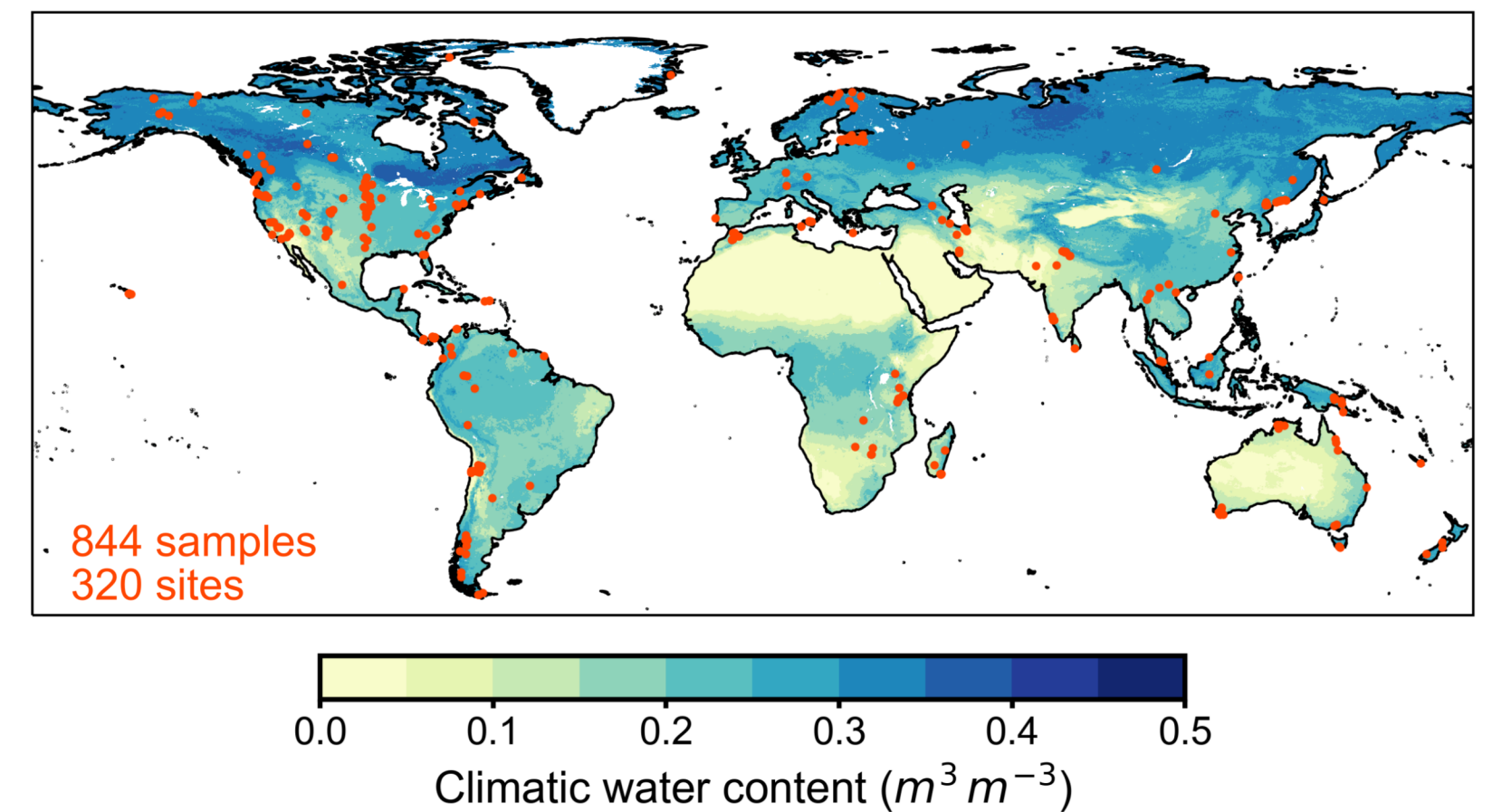


Fig. 3: Modeled spatial distribution of individual cells on soil surfaces with prescribed water content ($0.2 m^3 m^{-3}$) and carrying capacity ($2 \times 10^{17} m^{-3}$) after 7 days.

Sampling sites of soil bacterial diversity data^{2,3,4}



Richness = number of amplicon sequence variants ("species")
Abundance = relative proportion of species in *all* samples
Dominance = relative proportion of species in *one* sample
Ubiquity = probability of detecting a species in *any* sample

Proportions of rare and common species vary across terrestrial biomes

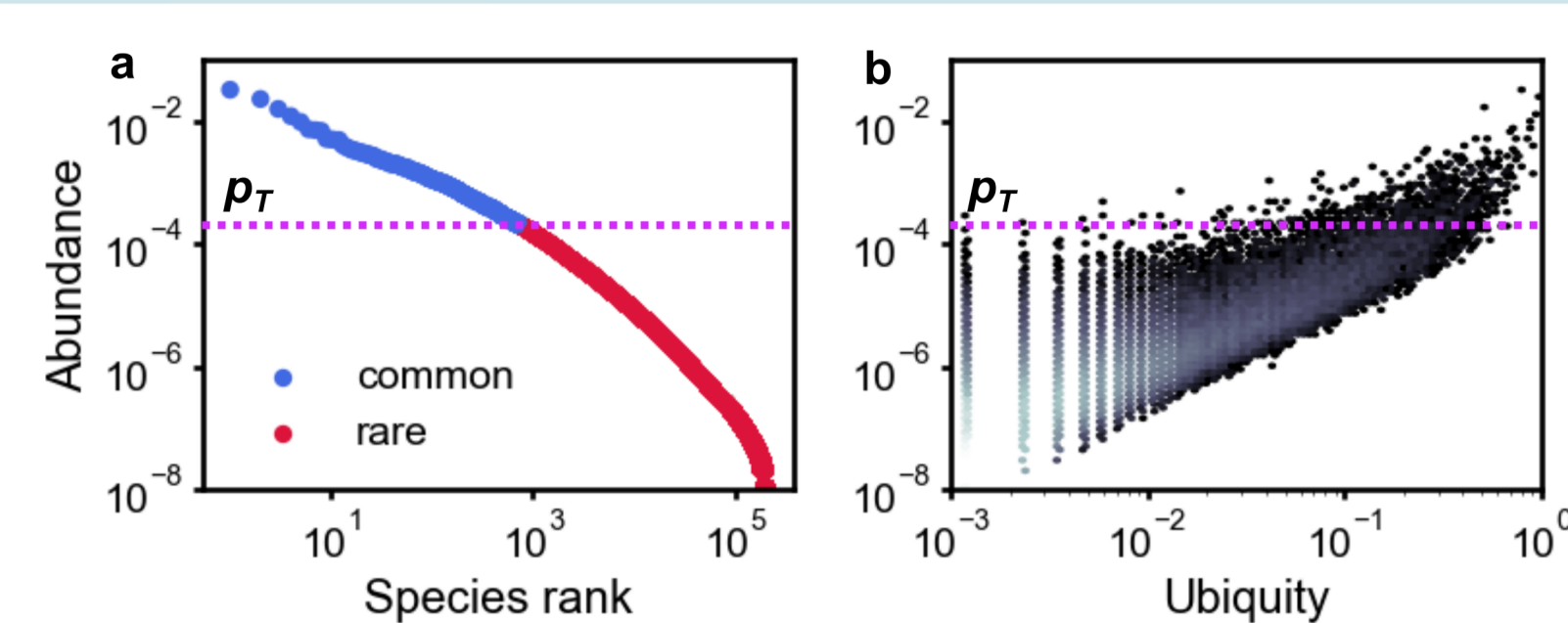
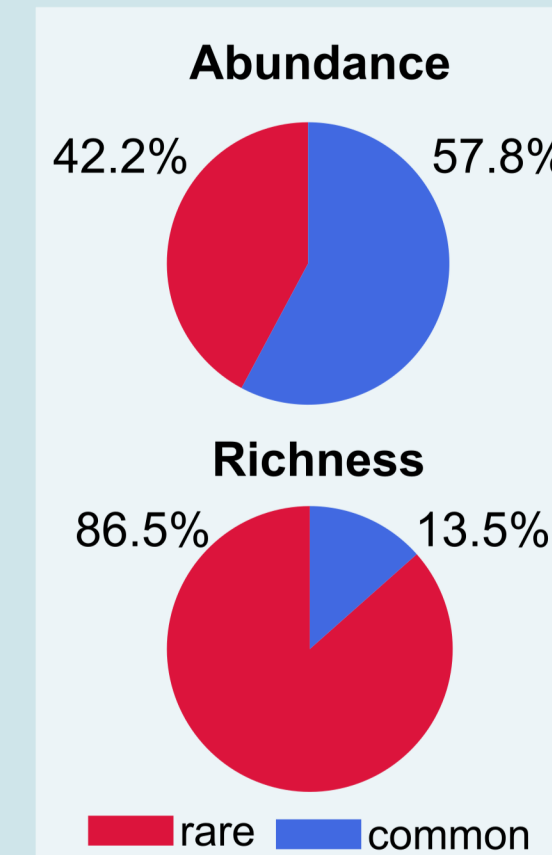


Fig. 4: Global species abundance and ubiquity are related. **a.** Common and rare species are defined based on a relative abundance threshold (p_r) relative abundance. Few species amount to a large proportion of the global distribution and many species are present at low abundances. **b.** Abundance and ubiquity are related. Species with high global relative abundance are also ubiquitous, i.e. are likely to occur in a larger



Only around **14%** of species are **common** but contribute to almost **60%** of **global relative abundance**.

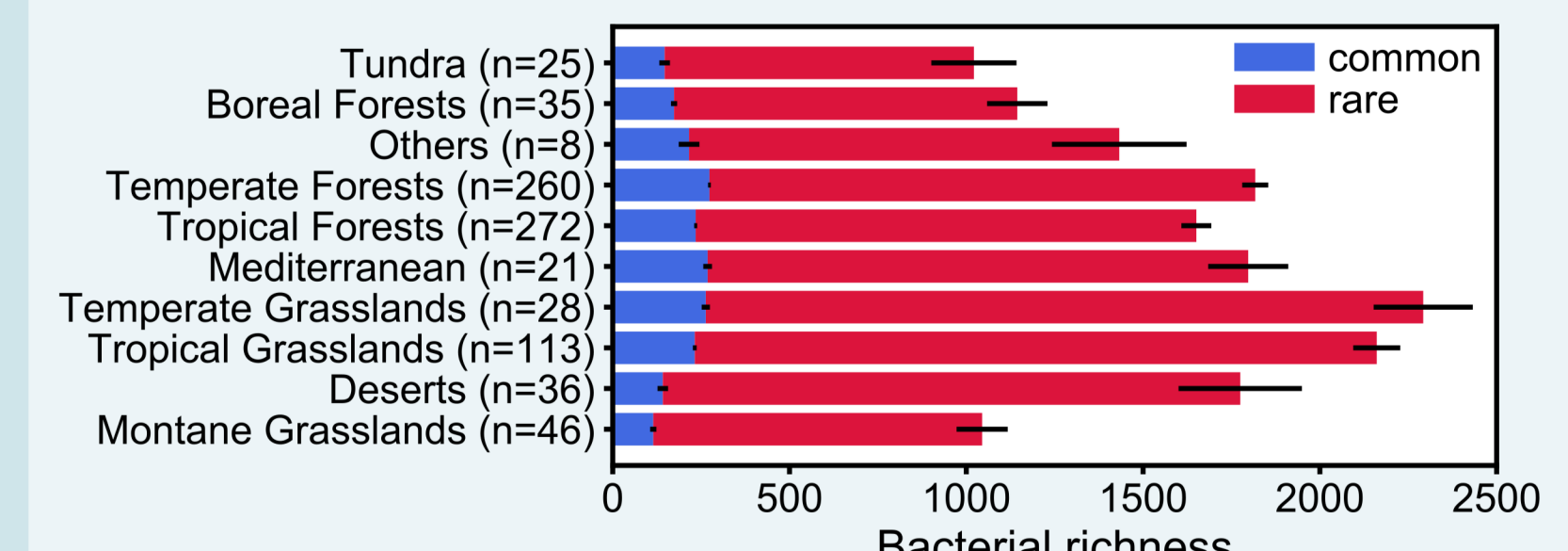


Fig. 5: Richness of common and rare soil bacteria for different biomes sorted in descending order based on climatic moisture condition. Rare species display stronger variation of mean bacterial richness among different biomes. Bars represent mean values with errorbars indicating standard errors for richness of common and rare species. Number of samples per biome are indicated.

>>> **Abundant species are also likely ubiquitous**

Rare species proportion declines with increased water content

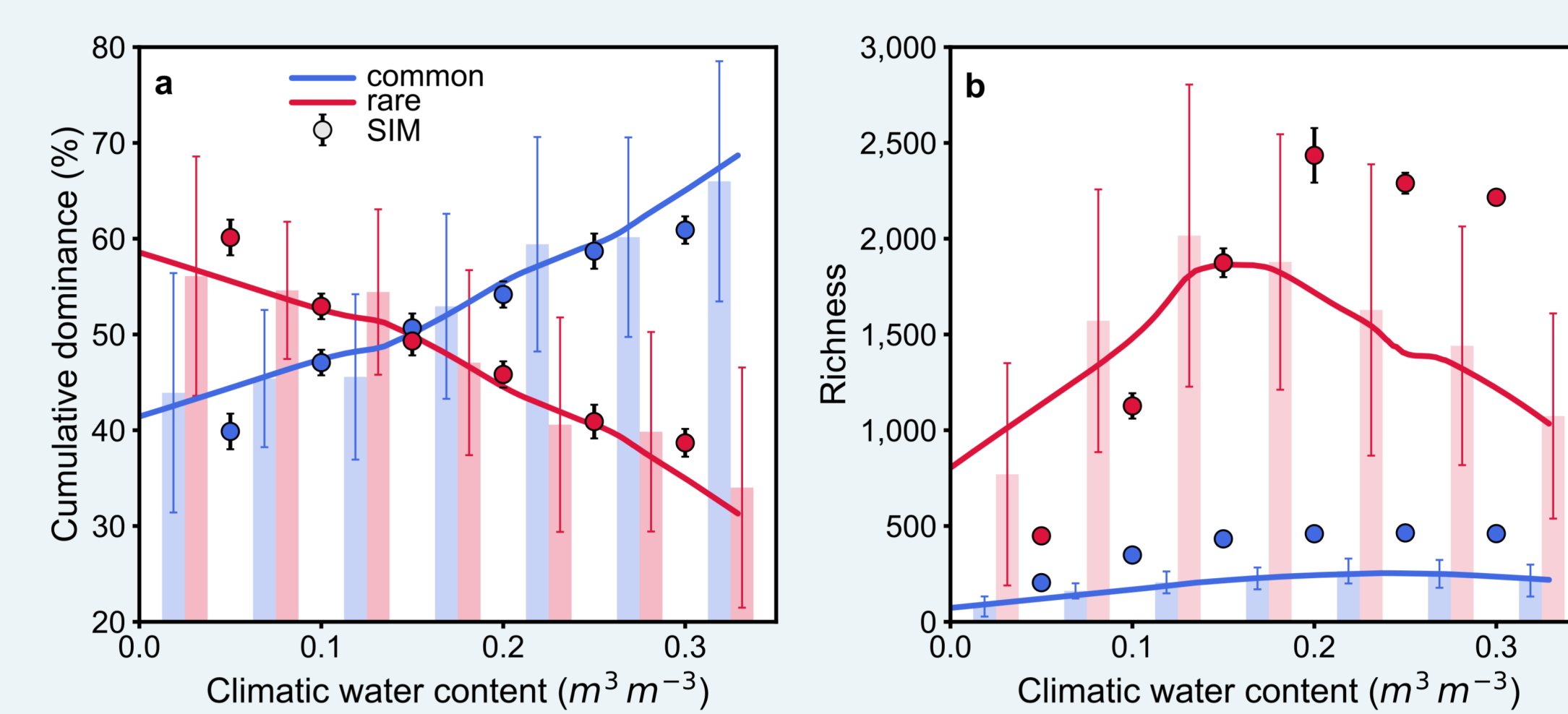


Fig. 6: Proportion and richness of rare and common species vary with climatic water content. Observational data^{1,2,3} and model results are compared. **a.** The cumulative dominance (percentage of community) that are common or rare. Bars represent mean values with errorbars given by standard deviation (grouped by climatic water content). The solid lines are locally weighted scatterplot smooths (LOWESS). Symbols represent the mean and standard deviation of SIM model predictions. A potential carrying capacity of $3 \times 10^{17} m^{-3}$ was prescribed in the simulations. **b.** Richness of the two groups show distinct relations with climatic water content in good agreement with model results of the SIM. Bars and errorbars represent mean and standard deviations, respectively.

>>> **Model results in agreement with observations suggest that rare species abundance declines at high climatic water contents**

Conclusions

- Bacterial richness is linked to soil and climate via climatic water contents and carrying capacity using an aqueous-phase fragmentation-based heuristic model (HM) (Fig. 1).
- A mechanistic, spatially-explicit individual based model (SIM) captures trends in carrying capacity with water contents with no prior assumptions about the relation (Fig. 2).
- Abundant species are ubiquitous and can thus be distinguished as common and rare based on a relative abundance threshold (Fig. 4).
- The largest proportion of the global species abundance (almost 60%) is contributed by only 14% of total bacterial species.
- Richness of rare and common soil bacteria vary among biomes (Fig. 5).
- Simulations using the SIM suggest that variations in prevalence and richness of rare and common soil bacteria could be attributed largely to water contents (Fig. 6)

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