Maximum entropy production, carbon assimilation, and the spatial organization of vegetation in river basins

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The spatial organization of functional vegetation types in river basins is a major determinant of their runoff production, biodiversity, and ecosystem services. The optimization of different objective functions has been suggested to control the adaptive behavior of plants and ecosystems, often without a compelling justification. Maximum entropy production (MEP), rooted in thermodynamics principles, provides a tool to justify the choice of the objective function controlling vegetation organization. The application of MEP at the ecosystem scale results in maximum productivity (i.e., maximum canopy photosynthesis) as the thermodynamic limit toward which the organization of vegetation appears to evolve. Maximum productivity, which incorporates complex hydrologic feedbacks, allows us to reproduce the spatial macroscopic organization of functional types of vegetation in a thoroughly monitored river basin, without the need for a reductionist description of the underlying microscopic dynamics. The methodology incorporates the stochastic characteristics of precipitation and the associated soil moisture on a spatially disaggregated framework. Our results suggest that the spatial organization of functional vegetation types in river basins naturally evolves toward configurations corresponding to dynamically accessible local maxima of the maximum productivity of the ecosystem.

ecohydrology | ecology | vegetation patterns

Vegetation patterns in river basins shift in response to changes in precipitation and temperature, whose local impact is linked to the soil and geomorphological structure of the basin (1, 2). Semi-arid ecosystems are particularly sensitive to these changes because of the sensitivity of the soil moisture dynamics to climate, soil, and vegetation conditions (3–5). Moreover, the drainage structure of river basins determines the aspect (i.e., orientation) of the hillslopes and the location of the snow line, which in turn heavily impact the radiation balance and the dynamics of the soil moisture (6–8).

Given the number of factors affecting the distribution of vegetation in a river basin, the implementation of optimization frameworks based on plant-scale or canopy-scale dynamics is rather problematic (9). The optimization of different objective functions has been suggested to control the adaptive behavior of plants and ecosystems (10–13), often without a compelling justification. Furthermore, a detailed investigation of microscopic dynamics is generally unnecessary for the analysis of the macroscopic state of open systems (14). Maximum entropy production (MEP) (13, 15, 16) provides a general thermodynamic framework directly applicable to the ecosystem scale. For stationary states of open nonequilibrium systems, MEP states are preferably selected among all attainable states because they can exist within a greater number of environments (17).

In this paper MEP is applied to the study of vegetation at the ecosystem scale [following the derivation of Dewar (9)], to specify the objective function controlling the organization of different functional vegetation types in a river basin. Applying MEP to the carbon balance implies considering the entropy production by photosynthesis, a process strongly related to plant transpiration, which is controlled by fluxes of water and energy. Thus, explicitly accounting for the entropy production on the carbon cycle of a river basin implicitly includes important effects of other fluxes such as radiation, rainfall, and latent heat in the production of entropy, although these fluxes are not explicitly included in the expression for entropy production.

Our system, for the application of MEP, consists of the vegetation of an entire river basin and the portion of soil in which carbon is stored as organic matter. Fig. 1 shows a scheme of the carbon balance in this system.

Photosynthesis captures atmospheric carbon, in the form of carbon dioxide, which is introduced into the system as carbohydrates. These carbohydrates are mainly used with two purposes.

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The first one is to maintain plant vital functions. Carbohydrates are thus used and degraded via autotrophic respiration that generates carbon dioxide, which is emitted to the atmosphere. The second purpose is to support plant growth and to repair damaged plant tissues. The damaged tissues fall down and become part of the soil organic matter, which is used by different organisms to support their vital functions. This heterotrophic respiration results in the emission of carbon dioxide back to the atmosphere.

Entropy production is evaluated as the product of the mass flux across the boundaries times the chemical potential of the substance transported, divided by the temperature at which the interchange takes place (19). For the case of the carbon cycle (9),

$$\sigma_{\text{system}} = \frac{1}{T} (P \mu_P - R_A \mu_R - R_B \mu_R),$$

where $$\sigma_{\text{system}}$$ is the entropy production rate of the system, $$P$$ is the photosynthesis rate, $$R_A$$ and $$R_B$$ are the autotrophic and heterotrophic respiration rates, respectively, $$\mu_P$$ is the chemical potential of the photosynthates, and $$\mu_R$$ is the chemical potential of the products of respiration (9). MEP states that the carbon cycle at the ecosystem scale is controlled by the maximization of $$\sigma_{\text{system}}$$. However, this expression can be simplified.

Assuming the chemical potentials of the autotrophic and heterotrophic respirations are equal,

$$\sigma_{\text{system}} = \frac{1}{T} (P \mu_P - (R_A + R_B) \mu_R).$$

In the steady state (achieved on timescales of the order of tens of years) the carbon flux of photosynthesis is compensated by the autotrophic and heterotrophic respiration fluxes $$P \approx R_A + R_B$$ (9). Introducing this relation in the expression for the entropy production rate:

$$\sigma_{\text{system}} = \frac{1}{T} (P(\mu_P - \mu_R)).$$

Finally, assuming isothermal transformations (a justification of this assumption is provided in SI Materials and Methods),

$$\sigma_{\text{system}} \propto P.$$ 

Therefore, maximizing the entropy production rate of the carbon cycle of a river basin is equivalent to maximizing canopy photosynthesis. Thus, the most probable state for vegetation, i.e., the one explaining its actual spatial organization, corresponds to the one maximizing canopy photosynthesis (9).

Results and Discussion

Fig. 2 shows the observed vegetation pattern of the URS basin (20) as well as the patterns obtained for several values of the annealing parameter ($$\theta$$) throughout the simulated annealing procedure. Because the data do not allow for a spatial distinction between Bouteloua gracilis and Bouteloua eriopoda, the two grass species taken as representatives of all of the grass species present at the basin, both types are merged together as grasses when comparing the simulated patterns with the observed ones. The simulated vegetation patterns correspond to steady states of the system for the prescribed annealing parameters.

Vegetation profiles provide an objective and quantitative comparison between the observed spatial distribution of vegetation types and the distribution obtained at different values of the annealing parameter. Fig. 3 shows the profiles of the different functional vegetation types as a function of the distance from the outlet, measured along the drainage network. The patterns of vegetation for $$\theta = 4 \times 10^{-3}$$ (Fig. 3, Right) show a very good agreement with the observed ones. Only the profile of the simulated
grasses in the upper part of the basin differs from the observed one. Fig. 3, Left also shows the vegetation profiles for $\theta=0$. Although the profiles for trees and shrubs are again very well reproduced, there is now a complete absence of grasses. The reduced accuracy in grass reproduction in one case and their complete absence for $\theta=0$ suggest that the presence of grasses in the real basin results from local conditions on soil and topography that preclude the vegetation pattern corresponding to the ground state ($\theta=0$) to dominate and instead lead to a feasible optimal pattern (21) corresponding to a temperature slightly larger than zero. Feasible optimality is also a concept found in the evolution of channel networks in river basins where networks are constrained to settle in suboptimal configurations corresponding to local (rather than global) minima of energy dissipation, an exact feature of steady-state landscape evolution equations in the small gradient approximation (22).

The productivity of the basin vegetation patterns associated with different temperatures of the simulated annealing procedure is shown in Fig. 4. The maximum productivity is achieved for $\theta=0$. The simulation best reproducing the existing vegetation structure, however, is obtained for $\theta=4 \times 10^{-3}$, which is very close to the absolute optimum.

A synthesis of river basin metabolism is contained in the allometric relationship between the total average transpiration in a subbasin and the total amount of runoff present on the average in the network of the same subbasin (18). Fig. 5 shows such a relationship for the observed vegetation organization of the URS basin and for that corresponding to the vegetation pattern associated with a maximum productivity (i.e., $\theta=4 \times 10^{-3}$) in the simulated annealing procedure.

The slope of the allometric relationship for the real basin ($0.672 \pm 0.1 \times 10^{-4}$) is almost identical to the slope of the optimal basin obtained in the simulations ($0.674 \pm 1.6 \times 10^{-4}$), presenting a very small difference (0.4%) between them. This behavior was expected because slope is controlled by the structure of the drainage network (23). The location of the line, however, depends on the proportionality constant between $T_i$ (the total transpiration in a subbasin) and $\Sigma A_i$ (the total amount of runoff present on average in a subbasin). This proportionality constant is in turn determined by the vegetation organization in the basin. Fig. 5 shows that the location of both lines is also very similar, the real basin presenting a proportionality constant of $12.734 \pm 0.026$ and the simulated one that of $13.159 \pm 0.020$ (a difference of 3.3%). As expected, the relationship for the optimal case is located slightly above the one for the real basin. The accuracy values presented above are equal to 1 SD, estimated using the bootstrapping method (24) on every variable studied.

The allometric relationships for the case of a basin covered by a random vegetation and that of a basin fully covered by B. gracilis are also presented in Fig. 5. In both cases the lines still exhibit a $2/3$ slope ($0.670 \pm 1.5 \times 10^{-4}$ for the random case and $0.664 \pm 1.0 \times 10^{-4}$ for the B. gracilis one). However, the
location of the lines is lower than in the optimal basin obtained in the simulations. The proportionality constants in these cases are $11.184 \pm 0.016$ for the former and $11.175 \pm 0.010$ for the latter. These values present a difference of approximately 12% compared with the real basin. This lower value of the proportionality constant indicates a lower efficiency of the basin in its use of the area it occupies to produce transpiration (or assimilation or entropy, which in this case are equivalent).

The agreement between the modeled and observed vegetation profiles, and also between the modeled and observed allometric relationships, suggests that the vegetation of river basins tends to organize around the maximum productivity thermodynamic limit, equivalent to the state of maximum entropy production in these far from equilibrium open systems.

The maximum productivity thermodynamic limit, derived and warranted by maximum entropy production, provides a framework to forecast changes in the organization of functional vegetation types in river basins arising from ongoing and future changes in precipitation and temperature patterns.

### Materials and Methods

Soil moisture dynamics and water balance are modeled at every 28.5 x 28.5-m$^2$ pixel of a grid covering the basin, by means of the steady-state probability distribution function of soil moisture (25, 26). It makes use of meteorological data (average rate of storm arrival, average storm depth, and average temperature) and of potential evapotranspiration values computed by means of the Penman–Monteith model to solve the stochastic water balance.

Meteorological data are obtained from six stations in the Rio Salado region (27). To distribute meteorological magnitudes over the basin, the variables measured only at the stations are correlated with variables measured for the whole basin. Rainfall characteristics (average rate of storm arrivals and average storm depth) are correlated with pixel elevation. Temperature and incoming shortwave solar radiation are correlated with pixel aspect and elevation (Fig. S1). This procedure serves to downscale the meteorological variables to the pixel scale. Details about the datasets and the methodologies of spatial downscaling are described in SI Materials and Methods.

Plant transpiration is obtained from the stochastic water balance and used to estimate plant assimilation (28–30). Computing plant transpiration by means of a stochastic model allows us to explicitly incorporate the randomness of precipitation as well as the spatially dependent characteristics of the climate, soil, and geomorphological structure of the watershed to investigate the impact of different patterns of the regional functional types of vegetation on the productivity of the basin. Because almost all assimilation in URS takes place during the growing season (31), the characterization of the hydrologic dynamics and its associated vegetation productivity are referred to the period from May to September.

The average productivity is estimated at each site and over the whole basin. The total ecosystem assimilation is obtained by summing up the individual assimilations at every pixel of the basin. Assimilation is computed by multiplying the average growing season transpiration at every pixel by the water use efficiency (WUE) of the vegetation type occupying the pixel. WUE values and the characteristics of the four predominant plant species in the URS basin that have been used for the numerical simulations (32) are presented in Tables S1 and S2. The spatial distribution of soil textures is shown in Fig. S2. Soil parameters (26, 33) associated with each of the three soil textures found within the basin are presented in Table S3.

The optimal vegetation distribution, i.e., the one maximizing ecosystem productivity, was obtained by means of a simulated annealing procedure (34, 35). The simulated annealing procedure defines a dimensionless

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**Fig. 4.** Assimilation vs. annealing parameter curve. The curve shows the steady-state value of assimilation attained by the vegetation patterns resulting from the simulated annealing procedure for every annealing parameter in the experiment schedule. The dot represents the simulation that compares best with the observations ($\theta = 4 \times 10^{-3}$).

**Fig. 5.** Allometric synthesis of river basin metabolism. Shown is total transpiration per subbasin vs. total amount of runoff present on average in the subbasin. The total amount of runoff present in the subbasin is the sum of the runoff of all of the links contained within the considered subbasin. The total amount of runoff is surrogated by the nested sum of total contributing areas (22). The exponent is very close to 2 (3), which in this case are equivalent).

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$$T_r \sim (\Sigma A_t)^{0.672}$$

$$T_r \sim (\Sigma A_t)^{0.674}$$

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$\theta = 4 \times 10^{-3}$

Grasses

Random
parameter, called the annealing parameter, which accounts for all of the different factors not explicitly included in the modeling and controls the features of the optimal configurations. For a given annealing parameter, the simulated annealing algorithm proceeds to tentatively update (i.e., change) the vegetation at a randomly chosen pixel by a vegetation type randomly chosen among those existing in the whole basin. If there is an increase of the total ecosystem assimilation with the updated vegetation, the change is accepted. If not, the change may be accepted with a probability

\[ p = e^{-\beta \Delta} \]  

that depends on the absolute value of the decrease in total ecosystem assimilation (\( \Delta \)) and the annealing parameter (\( \beta \)). The constant \( \beta \) is assigned a value of 1 and is measured in the same units of assimilation (kg CO2/d). It serves to transform the temperature into a dimensionless parameter.

As a consequence of the formulation of the acceptance probability, when \( \beta = 0 \) (cold system), changes are accepted only if they increase total system productivity (therefore fulfilling the maximum productivity thermodynamic limit). This process leads to the vegetation distribution ground state for the basin under the imposed constraints and climatic conditions. When temperatures of the simulated annealing process are larger than 0, changes decreasing the overall productivity may be accepted with a prescribed probability (Eq. 1), depending on the magnitude of the decrease. For large values of the temperature parameter, its effect dominates over the effect of the driving thermodynamic limit (maximum productivity). In these situations a random vegetation organization is obtained (Fig. 2D).

For the purpose of this study a large number of different vegetation configurations over the basin as well as their corresponding productivities are analyzed for a set of temperatures. This procedure allows us to consider different degrees of disruption to the optimal solution corresponding to the different strengths of constraints affecting dynamic accessibility.

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The Upper Rio Salado river is a constant of: and presents elevations ranging from 1

Δ

f1o f4
e the is the absolute value of the change, 

j

×

(M E P )s t a t e . T h i s b e h a v i o r i s k n o n

every pixel of the basin. The state reached by many natural systems, however close, may not be the optimum state, e.g., the maximum entropy production (MEP) state. This behavior is known as feasible optimality (2). The concept of feasible optimality accounts for all those factors that are not explicitly included in the analysis of a system, preventing the system from attaining its optimal state of operation. In this work the maximization of productivity is carried out via a simulated annealing procedure to account for feasible optimality.

When applied to the optimization of canopy photosynthesis, simulated annealing is carried out as follows. An initial state is assigned to the system, in our case a random vegetation organization in the basin (Fig. 2D). The annealing parameter is initially set to a large value for which the random vegetation distribution constitutes a steady state (θ larger than 1.0 in the URS). Then an iterative process is started. At every iteration, the vegetation type at a randomly chosen location is tentatively changed to a new vegetation type, randomly selected among the other possible ones potentially existing in the basin. The tentative change is accepted if it increments canopy photosynthesis, i.e., productivity or assimilation. In the case that it decreases assimilation, the change may be accepted with probability

\[ p = e^{-\Delta / \theta} \]

where Δ is the absolute value of the change, φ is a constant of value 1 with units of assimilation, and θ is the dimensionless annealing parameter of the simulated annealing procedure. The larger the annealing parameter is, the more probable it is that a change will be accepted. Once a steady state for assimilation has been attained (it takes an average of 25 million iterations in the case of the URS), the annealing parameter is decreased and the process repeated until all of the parameters in the experiment schedule have been tested. As a result, the optimization process produces a steady-state solution for every different value of the annealing parameter of the system.

Isothermal Assumption. In the main text, to simplify the expression of the system’s entropy production, it is assumed that the transformations are isothermal. This assumption implies that at a given location of the basin, the temperature at which photosynthesis and respiration take place is constant and independent of the type of vegetation populating the site. Thus, different rates of entropy production at a site become dependent only on the vegetation type controlling the carbon cycle at that site.

In any case, the contribution from temperature variations would be small. At the URS there exists a 1,000-m difference in elevation between the outlet and the highest point. This difference in elevation induces a difference in temperature of about 10 °C, that is, temperatures ranging approximately from 285 K (12 °C) to 295 K (22 °C). Therefore, the maximum difference introduced by temperature in the computation of entropy production would be about 3.5%.

Assimilation Computation. The relation between the flux of carbon dioxide entering the plant and the flux of water vapor lost to the atmosphere during the transpiration process may be measured by means of the water use efficiency (WUE). WUE is normally expressed in [mmol CO₂ · mol⁻¹ H₂O]. Considering 1 mol of CO₂ is 44 g of CO₂, and 1 mol of H₂O is 18 g, WUE can be expressed in [g CO₂ · g⁻¹ H₂O], multiplying by (44/18) × 10⁻³ (Table S1). Transpiration times water use efficiency provides the mass of CO₂ fixed by square meter and day [kg CO₂ · d⁻¹ · m⁻²]. Multiplying by the surface area of a pixel, the total mass of CO₂ the pixel fixes daily is obtained. As only 18 g of carbon is present in the 44 g of carbon dioxide, the mass of CO₂ previously obtained is multiplied by (12/44) to obtain the amount of carbon fixed daily by the pixel considered.

The assimilation at every pixel is thus computed as the product of the average transpiration of the pixel (derived from the hydrologic model described later) and the WUE of the functional vegetation type populating the pixel.

Study Site and Input Data Description. The URS is located within the Sevilleta Long-Term Ecological Research (LTER) site, adjacent to the Cibola National Forest, New Mexico. It covers an area of 466 km² and presents elevations ranging from 1,985 m above mean sea level (a.s.l.) to 2,880 m a.s.l. It is a semiarid environment with a growing season from May to September.

A digital elevation model (DEM) for the basin with a resolution of 1 arc-second was obtained from the US Geological Survey National Elevation Dataset (3, 4). A 1-arc-second resolution map of soil texture distribution was obtained from the US Department of Agriculture (USDA) STATSGO soil database (5) (Fig. S1). Soil parameters are presented in Table S3.

Soil cover data were obtained from the 1-arc-second resolution US Geological Survey National Land Cover Dataset (6) (NLCD) derived from Landsat imagery (Fig. 24). Soil cover data indicate the spatial distribution of different functional vegetation types in the basin, without distinction of species. Trees (Pinus-Juniper woodland), shrubs (mainly Larrea tridentata), and grasses (Black Grama, Bouteloua eriopoda; and Blue Grama, Bouteloua gracilis) are the dominant species in the URS. Their key functional characteristics are shown in Table S2.

Data from six meteorological stations (7) (stations 40–45) with hourly records from 1987 to 2010 were used to characterize daily averages of rainfall, vapor pressure, relative humidity, air temperature, wind speed, and incoming shortwave solar radiation. Growing season averages were determined for every variable at every meteorological station. Rainfall is modeled as a marked Poisson process on a daily scale (2). It is characterized by two
parameters: the frequency of rainy days during the growing season, \( \lambda \) (\( \text{d}^{-1} \)), and the average storm depth, \( \alpha \) (\( \text{mm} \)), which is assumed to have an exponential distribution. \( \lambda \) and \( \alpha \) are calculated for every station and a regression with the elevation of the station is obtained for each parameter. These regressions (shown below, where \( Z \) is elevation above mean sea level [\( \text{m} \)] serve to down-scale the rainfall parameters across the whole basin, assigning a \( \lambda \)- and an \( \alpha \)-value to every pixel of the basin:

\[
\begin{align*}
\lambda &= 0.1077 + 6.75 \times 10^{-5} \cdot Z \quad \text{\( R^2 = 0.586 \)} \\
\alpha &= 1.649 + 0.0038 \cdot Z \quad \text{\( R^2 = 0.835 \)}
\end{align*}
\]

A regression was established by relating growing season average air temperature and two station variables: elevation and measured growing season average incoming shortwave solar radiation. The resulting regression is shown below, where \( Z \) is elevation above mean sea level [\( \text{m} \)] and \( \text{SW}_{inc} \) is incoming shortwave solar radiation [\( \text{J} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)]:

\[
T_e = 27.6 - 0.0068Z + 0.0176 \cdot \text{SW}_{inc} \quad \text{\( R^2 = 0.57 \)}
\]

At every pixel the above regression requires \( \text{SW}_{inc} \) values to compute air temperature. A daily incoming shortwave radiation (ISR) is modeled for every pixel of the basin, using the r.sun (8) module of the GRASS GIS software (9). ISR calculation accounts for pixel location, aspect, and shading effects. A growing season average for ISR is calculated by averaging the values at mid-May, mid-June, and mid-August. A dimensionless coefficient (\( k_{ISR} \)) is defined at every pixel by dividing its growing season average ISR value by the growing season ISR basin average (Fig. S2). The growing season average \( \text{SW}_{inc} \) for every pixel of the basin is computed multiplying its \( k_{ISR} \) by the growing season average incoming shortwave solar radiation, computed for the whole basin from the measured values at the meteorological stations.

Hydrologic Modeling. The hydrologic modeling at the daily scale is based in the full computation of the stochastic water balance at every pixel through the probability density function (pdf) of soil moisture (10, 11). In the modeling scheme evapotranspiration is assumed to be an increasing function of soil moisture, ranging from zero, for soil moisture values below the hygroscopic point, to a maximum at the potential evapotranspiration (PET), when soil moisture reaches values larger than those corresponding to incipient stomata closure.

The wilting point and the soil moisture corresponding to incipient stomata closure are functions of soil texture and plant type. PET is evaluated by means of the Penmann–Monteith model and depends on climatic conditions and vegetation characteristics. For the computation of net radiation it is assumed that, at any given site, canopy and air temperatures are equal (12). Canopy conductance is evaluated as the product of the leaf area index and the maximum stomatal conductance. The aerodynamic atmospheric conductance is evaluated considering wind speed and plant dimensions. Vapor pressure and vapor pressure gradients are evaluated from meteorological data. PET is estimated at the daily scale, considering the average length of a day during the growing season at the URS.

The steady-state components of the water balance at the daily scale are solved by integrating the stochastic differential equation (SDE) of soil moisture (10, 11). A previous study in the URS (13) pointed out the importance of the initial condition of soil moisture at the start of the growing season to correctly evaluate the average value of the different components of the water balance at each site of the basin. The initial condition is controlled by the snowmelt accumulated in the soil at the beginning of the growing season. This initial condition creates an initial transient regime that is not captured by the steady-state soil moisture pdf. After this initial regime, the steady-state pdf is a valid representation of the physical processes taking place (11).

In this paper the initial soil moisture at each site at the start of the growing season is evaluated by accounting for the water equivalent of the snow (SWE) infiltrated into the soil. It is assumed that a site, i.e., a pixel, (i) located at the snow line, i.e., 2,300 m, (ii) colonized by tree vegetation, and (iii) presenting silt loam soil texture starts the growing season under saturation conditions. This assumption implies 502 mm of SWE must be present at the site. Above the snow line, a constant 502 mm SWE is assumed. Below it, an exponential decay is assumed, given by the equation

\[
W = \hat{W} \cdot e^{-k(H-z)},
\]

where \( W \) is the SWE at elevation \( z \), \( \hat{W} \) is the saturation SWE (502 mm), \( H \) is the height of the snow line (2,300 m), and \( k \) is the decay constant (0.01).

The SWE so obtained is modified to account for the effect of site orientation, i.e., aspect. To this effect SWE is divided by the solar radiation coefficient \( k_{ISR} \) (Fig. S2). This operation increases SWE in shaded sites and reduces it in exposed sites. The initial soil moisture is then computed, assuming SWE is equally distributed over the volume of the soil pores, i.e., the product of average root depth and soil porosity.

The duration of the transient regime is evaluated by computing the mean first passage time (14) (MFPT) that the soil moisture takes to go from its initial value to the first descending cross below the threshold corresponding to incipient stomata closure.

During the transient regime plants evapotranspire at the potential rate (PET). Afterward, evapotranspiration is provided by the average steady-state solution. The growing season evapotranspiration is evaluated as a weighted average between evapotranspiration during the transient and that during the steady regimes (11), as expressed in the equation

\[
\overline{ET}_{GS} = \frac{1}{T_{GS}} \left[ MFPT \cdot PET + (T_{GS} - MFPT) \overline{ET}_{SS} \right]
\]

where \( \overline{ET}_{GS} \) is the average growing season evapotranspiration, \( \overline{ET}_{SS} \) is the average steady-state evapotranspiration, and \( T_{GS} \) is the growing season length in days.

Average growing season transpiration is then evaluated by subtracting bare soil evaporation from the average growing season evapotranspiration. Bare soil evaporation is assumed constant and equal to \( \alpha \) for the whole basin.


Fig. S1. Spatial distribution of $k_{irr}$. Spatial distribution of the irradiation coefficient at the basin is shown. The coefficient accounts for relief shading effects.

Fig. S2. Spatial distribution of the main three soil textures present at the upper Rio Salado basin.

| Vegetation cover          | WUE $|\text{mmol CO}_2 \cdot \text{mol}^{-1} \text{H}_2\text{O}|$ | WUE $|\text{g CO}_2 \cdot \text{g}^{-1} \text{H}_2\text{O}|$ |
|---------------------------|-------------------------------------------------|-------------------------------------------------|
| Pinyon–Juniper            | 5.84                                            | $14.27 \times 10^{-3}$                          |
| Larrea tridentata         | 8.40                                            | $20.53 \times 10^{-3}$                          |
| Bouteloua gracilis       | 4.10                                            | $10.02 \times 10^{-3}$                          |
| Bouteloua eriopoda       | 4.30                                            | $10.51 \times 10^{-3}$                          |

The values are representative averages over the growing season. Tree data (Pinyon–Juniper) were provided by Jean-Marc Limousin, University of New Mexico. Shrub data (Larrea tridentata) were provided by Juliana Medeiros, University of Kansas. Grass data (Bouteloua gracilis and Bouteloua eriopoda) were provided by Michell L. Thomey, University of New Mexico.
Table S2. Vegetation parameters

<table>
<thead>
<tr>
<th>Vegetation cover</th>
<th>$\Psi_w$ [MPa]</th>
<th>$\Psi^*$ [MPa]</th>
<th>$\alpha_s$ [-]</th>
<th>$g_{\text{MAX}}$ mmol/m²s</th>
<th>LAI: m²/m²</th>
<th>$H$ [m]</th>
<th>$Z_r$ [cm]</th>
<th>$d$ [mm]</th>
</tr>
</thead>
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<tr>
<td>Pinyon-Juniper</td>
<td>-2.8</td>
<td>-0.5</td>
<td>0.10</td>
<td>150</td>
<td>1.50</td>
<td>4.00</td>
<td>150</td>
<td>2.0</td>
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<td>Larrea tridentata</td>
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<td>-0.4</td>
<td>0.15</td>
<td>180</td>
<td>0.50</td>
<td>1.00</td>
<td>40</td>
<td>1.5</td>
</tr>
<tr>
<td>Bouteloua gracilis</td>
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<td>-0.1</td>
<td>0.12</td>
<td>400</td>
<td>0.25</td>
<td>0.50</td>
<td>30</td>
<td>1.0</td>
</tr>
<tr>
<td>Bouteloua eriopoda</td>
<td>-4.5</td>
<td>-0.1</td>
<td>0.12</td>
<td>300</td>
<td>0.40</td>
<td>0.65</td>
<td>35</td>
<td>1.0</td>
</tr>
</tbody>
</table>

$\Psi_w$ is the wilting-point matric potential, $\Psi^*$ is the matric potential for incipient stomata closure, $\alpha_s$ is the shortwave albedo, $g_{\text{MAX}}$ is the maximum stomatal conductance, LAI is the leaf-area index, $H$ is the average vegetation height, $Z_r$ is the average root depth, and $d$ is the canopy interception. Data for Pinyon-Juniper, Larrea tridentata, and Bouteloua gracilis are taken from a previous study of Rio Salado (1). Bouteloua eriopoda individuals are larger than B. gracilis ones (2). This fact has been taken into account by modifying the size parameters of B. Eriopoda ($H$ and $Z_r$) as well as $\Psi_w$, $g_{\text{MAX}}$, and LAI.


Table S3. Soil parameters for the soil textures present in the basin

<table>
<thead>
<tr>
<th>Soil type</th>
<th>$\Psi_h$ [MPa]</th>
<th>$\Psi_{sat}$ [MPa]</th>
<th>$s_h$ [-]</th>
<th>$s_{tc}$ [-]</th>
<th>$K_s$ [cm/d]</th>
<th>$n$ [-]</th>
<th>$b$ [-]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silt loam</td>
<td>-10.0</td>
<td>$-5.55 \times 10^{-3}$</td>
<td>0.24</td>
<td>0.69</td>
<td>25.0</td>
<td>0.485</td>
<td>5.30</td>
</tr>
<tr>
<td>Loam</td>
<td>-10.0</td>
<td>$-1.43 \times 10^{-3}$</td>
<td>0.19</td>
<td>0.54</td>
<td>20.0</td>
<td>0.451</td>
<td>5.39</td>
</tr>
<tr>
<td>Sandy loam</td>
<td>-10.0</td>
<td>$-7.04 \times 10^{-3}$</td>
<td>0.14</td>
<td>0.44</td>
<td>80.0</td>
<td>0.435</td>
<td>4.90</td>
</tr>
</tbody>
</table>

$\Psi_h$ is the hygroscopic point matric potential (1), $\Psi_{sat}$ is the saturation point matric potential (1), $s_h$ is the hygroscopic point relative soil moisture (1), $s_{tc}$ is the relative soil moisture at field capacity (1), $K_s$ is the saturated hydraulic conductivity (2), $n$ is the porosity (1), and $b$ is the pore distribution index (1).