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RESEARCH
REVIEW

ET come home: potential evapotranspiration in geographical ecology

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ABSTRACT

Aim Many macroecological analyses are based on analyses of climatological data, within which evapotranspiration estimates are of central importance. In this paper we evaluate and review the use of evapotranspiration models and data in studies of geographical ecology to test the likely sensitivity of the analyses to variation in the performance of different metrics of potential evapotranspiration.

Location Analyses are based on: (1) a latitudinal transect of sites (FLUXNET) for 11 different land-cover types; and (2) globally gridded data.

Methods First, we review the fundamental concepts of evapotranspiration, outline basic evapotranspiration models and describe methods with which to measure evapotranspiration. Next, we compare three different types of potential evapotranspiration models – a temperature-based (Thornthwaite type), a radiation-based (Priestley–Taylor) and a combination (Penman–Monteith) model – for 11 different land-cover types. Finally, we compare these models at continental and global scales.

Results At some sites the models differ by less than 7%, but generally the difference was greater than 25% across most sites. The temperature-based model estimated 20–30% less than the radiation-based and combination models averaged across all sites. The combination model often gave the highest estimates (22% higher than the radiation-based model averaged across all sites). For continental and global averages, the potential evapotranspiration was very similar across all models. However, the difference in individual pixels was often larger than 150 mm year^{-1} between models.

Main conclusions The choice of evapotranspiration model and input data is likely to have a bearing on model fits and predictions when used in analyses of species richness and related phenomena at geographical scales of analysis. To assist those undertaking such analyses, we provide a guide to selecting an appropriate evapotranspiration model.

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Continental scale, evaporation, evapotranspiration, land cover, Penman–Monteith, Priestley–Taylor, Thornthwaite, transpiration.

INTRODUCTION

Evapotranspiration (ET) is often found to be one of the best climatic correlates of species richness (Currie, 1991; O'Brien, 1993, 1998; Diniz-Filho *et al.*, 2003; Hawkins & Porter, 2003; Hawkins *et al.*, 2003; Kreft & Jetz, 2007), and has also been used in predictive models of species richness for global application (O'Brien, 1998; Field *et al.*, 2005). ET data have been used and found to have explanatory power in other areas of geographical ecology and biogeography including, for example, analyses of traits such as body size (Medina *et al.*, 2007; Olalla-Tárraga & Rodríguez, 2007) and predicted range shifts as a consequence of future climate change (Midgley *et al.*, 2002). ET estimates provide an indication of ecologically important aspects of climate linked to energy supply and, depending on which form of ET is considered, to water balance and plant

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productivity (Rosenzweig, 1968; Currie, 1991; O'Brien, 1993, 1998, 2006).

How one chooses a model to estimate ET depends not only on how important the potential controls are for the system of study, but also on what data are available to run the model. We provide here: (1) a general description of the basics of ET; (2) a brief review of the use of ET in the macroecological and biogeographical literature; (3) an outline of different types of ET models, including an evaluation of their strengths and weaknesses; (4) an introduction to techniques of measuring ET; and (5) general guidelines for using ET in geographical ecology. We focus primarily on potential evapotranspiration (PET), but include discussion on actual evapotranspiration (AET) where appropriate. Our aims are:

1. To provide a comparative review of ET metrics for macroecologists and biogeographers.

2. To illustrate when, where and why different ET models converge and diverge in their estimates at local, regional and global scales.

3. To provide a guide to choosing an ET model for use in geographical ecology.

Basics of evapotranspiration

ET is the transfer of liquid water from open water and through plant transpiration to the atmosphere as water vapour. Sublimation, which is the transition of solid water (i.e. ice, snow) to vapour due to low atmospheric pressure (i.e. high altitude), dry air and high sunlight, is generally considered separate from ET. Sources of open water evaporation could include oceans, seas, lakes, rivers, ponds, puddles and water on objects such as plants, buildings, rocks, the soil surface (including movement of water through the soil to the surface) or in the context of measuring devices such as a pan. Transpiration is the loss of water vapour through pores called stomata located on leaves/needles or stems. Plants regulate the opening and closing of their stomata to minimize water loss (closed), yet maximize CO_2 absorption (open) for photosynthesis (Zeiger, 1983).

Energy is required to break the strong bonds that hold water molecules together as a liquid – when those bonds break, the individual water molecules may enter the surrounding atmosphere as vapour. If the liquid contains other substances (impurities), then it may have a lower capacity for evaporation (Marek & Straub, 2001). Energy may be in the form of heat, radiation or pressure. Regardless of the availability of energy, water molecules may not be able to enter the atmosphere if the atmosphere is already saturated with moisture (humidity) or if there is no wind (this is not to be confused with the buoyant vertical movement of gas molecules due to free convection) to facilitate the transfer of the molecules from the water source to the atmosphere. The wind itself may be differentially influenced by friction as it passes over smooth versus rough surfaces. Therefore, solar radiation (or, indirectly, air temperature), air humidity and wind speed are the main climate influences on ET (Monteith, 1981; Raupach, 2001). The main vegetative controls include leaf and canopy characteristics, regulation of stomata and rooting dynamics. Finally, soil characteristics control soil moisture retention of precipitation inputs. All of these potential controls vary in influence depending on the system in question, as well as the associated spatial and temporal scales of analysis.

If the atmosphere is not saturated and there is plenty of liquid water at the surface, and there is also sufficient wind to allow transfer of water vapour from the surface to the atmosphere, then it follows that ET will increase with increasing energy provided. Hence *actual* ET (AET) levels reflect both the energy regime *and* the water regime, and thus AET is best understood as a water balance variable (Budyko, 1971), which is broadly indicative of plant productivity (Rosenzweig, 1968; Donohue *et al.*, 2007). If there is no water, there is still a *potential* for ET to occur were water to be added to the system. This potential ET (PET) is a useful concept both for practical application and for scientific – especially ecological – application. In ecological research, PET provides a measure of the energy regime that reflects the capacity for transpiration flow and primary production in circumstances where water is not limiting.

For agriculturalists, accurate estimates of PET can provide knowledge of how much irrigation may be required, for instance, so that crops can maximize photosynthesis without suffering from drought or waterlogged soils (Allen, 1996). PET is often calculated initially for well-watered short grass (called the reference crop), then multiplied by a constant called a crop coefficient to represent the species and developmental stage. Water may be added to crops so that the AET matches the PET, but, by definition, AET never exceeds PET.

PET and AET should not be used interchangeably. The PET of the Sahara Desert, for example, is very high because it is hot, windy and dry, but because there is very little water the AET is very low. Moreover, the PET of the arctic tundra is very low because there is little radiation and heat, and the AET is also very low. Both the desert and tundra may have similar values of AET, but very different values of PET and very different ecosystems, functional ecology and diversity.

Hence it can be appreciated that AET and PET measure related but very distinct aspects of the climatological regime (and in the case of AET other aspects, e.g. soil, vegetation cover): PET being essentially an energy variable, while AET reflects the water balance of a place (Stephenson, 1990, 1998). Still, AET and PET are complementary to one another: while AET declines as a wet environment dries, PET increases because the energy that would have been used to drive AET is now available energy in the system (Bouchet, 1963; Morton, 1983). Conversely, a wetter surface can absorb more energy, thus leaving less available energy to drive PET, which is an energy variable. In practice, whilst it is possible to estimate PET using quite simple devices, such as evaporation pans, it is inherently more difficult to measure AET, as it requires sophisticated scaling techniques or expensive micrometeorological eddy flux instrumentation.

Evapotranspiration in the ecological literature

The ecological literature includes large numbers of papers using climatic variables for many different purposes, prominent among which are efforts to relate species diversity to climatic and other potential causal variables. Within the macroecological and biogeographical literature, a wide array of different moisture and energy regime variables has been deployed. Prominent amongst the former are annual or seasonal precipitation, and amongst the latter, annual or seasonal temperature and PET. AET is sometimes classed with the former (water variables) and sometimes the latter (energy variables), but for plants at least, with their dependence on solar energy, thermal conditions within which water is in its liquid state, and on the availability of water, AET is best viewed as a composite water–energy variable (Stephenson, 1990, 1998; O'Brien, 1993, 1998).

For the reasons given above, AET provides only a crude index of the conditions for plant growth. Hence, for many purposes and applications it is preferable to use separate water and energy variables in geographical ecological modelling. For example, in analyses of species richness patterns of woody plants in southern Africa at the macroscale, E. M. O'Brien and colleagues showed that while AET provided higher statistical power on its own than did PET, a two-variable model based on annual rainfall and minimum monthly PET (i.e. Thornthwaite) provided a much stronger basis for building a much more effective general predictive model (O'Brien, 1993, 1998, 2006; Field *et al*., 2005). The ecological significance of water–energy dynamics and the distinction between AET and PET in this context is discussed in depth by O'Brien (1998, 2006).

For geographical ecology PET is therefore in theory a less ambiguous variable than AET. While AET can often describe more variation in, for example, species richness than PET on its own, when combined in models with water regime variables PET can arguably provide a more powerful and flexible input in model building (see O'Brien, 1998; Field *et al*., 2005). However, there are many different methods of calculating both AET and PET, meaning that in practice different authors are using metrics with varying properties. For instance, in analyses of coarse-scale spatial patterns in species richness, authors have used PET equations provided by Budyko (1978) (Currie, 1991; Kerr & Packer, 1997, 1999), by Thornthwaite (1948) (O'Brien, 1993, 1998; O'Brien *et al*., 1998, 2000; Field *et al*., 2005; Zhao *et al*., 2006), by Priestley & Taylor (1972) (Hawkins & Porter, 2003; Anderson *et al*., 2007), by Holdridge (1947) (Bhattarai & Vetaas, 2003; Bhattarai *et al*., 2004) or other formulae described to varying degrees of clarity (e.g. less clearly described: Hoffman *et al*., 1994; well described: van Rensburg *et al*., 2002).

While these analyses span varying taxa, including freshwater fish, amphibians, invertebrates, plants, birds and mammals, which inevitably require separate models to be developed, where efforts have been made to evaluate the same general model structure for a single taxon (cf. Hawkins *et al*., 2003) comparability may be hampered by the use of different forms of climate data and the use of different PET metrics. For example, see and contrast the papers (cited above) by O'Brien and colleagues, by Currie, and by Bhattarai and colleagues: all are on plants, each team using a different favoured PET method. Similar variability exists in the use of different formulae for estimating AET (for four different choices see Currie, 1991, Hawkins & Porter, 2003, Mönkkönen *et al*., 2006, and Zhao *et al*., 2006). A fuller consideration of the interpretation of AET and its value as a proxy for net primary productivity may be found elsewhere (Rosenzweig, 1968; Stephenson, 1990, 1998).

A SIMPLE GUIDE TO ET METRICS

ET models

Water balance

If we consider a watershed (or any other type of 'closed' system, including the Earth), where the only water input is from precipitation (P), then the only paths that water can take (not counting human systems or extraction by animals and insects, or leakage into Earth's deep crust) are into the soil as groundwater recharge/flow (D), surface runoff through streamflow (Q), stored in standing water (i.e. lakes, ponds) and in, or on, plants (S), or back to the atmosphere (AET). The precipitation is therefore 'balanced' by the sum of these respective destinations:

$$P = D + Q + S + \text{AET}. \tag{1}$$

We may be able to measure P from rain gauges, D from monitoring wells, Q from stream measurements and the change in S from water body volumes, but we may not be able to measure AET. Hence, AET can be calculated (commonly at a monthly time step) from the four known measurements. Because of the large spatial scale on which the water balance equation is often applied, it may be difficult to measure all terms accurately and to 'close' the equation (the left-hand side of the equation should equal the right-hand side of the equation). The water balance equation is for AET only: PET may be much larger, but there is no indication from the equation; AET may equal PET when the water supply is sufficiently large.

Energy balance

Energy coming from the sun less any radiation that gets reflected (or emitted as thermal infrared radiation) back to the atmosphere – or, net radiation (R_n) – is energy available for AET. Some of that R_n we can feel as the sensible heat flux (H), some of it is stored in the soil (G_1) and other objects such as woody material (G_2),[1] and the rest of the energy is absorbed by water (less than 1% of R_n is used in photosynthesis; Twine *et al*., 2000), which can be converted to vapour for AET. A certain amount of energy per mass of water is required to vaporize water, and this is called the latent heat of vaporization. AET, considered as the energy[2] required to drive it, is often called the latent heat of

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[1] The nomenclature is usually S, but we do not use it to avoid confusion with the same nomenclature from equation 1.

[2] Water fluxes such as precipitation and ET are usually given in units of depth per time (i.e. mm day^{-1}); the units are consistent when they are in volume per area per time (i.e. m^3 ha^{-1} day^{-1}). 1 m^3 is equal to 1000 litres. Water can also be expressed in units of mass – 1 kg of water is equal to 1 mm of water spread over 1 m^2. ET, like R_n, can be expressed in units of

evaporation.[3] When liquid water becomes vapour it absorbs heat, causing a drop in temperature in its surroundings. AET removes the most energetic vapour molecules from the liquid, which reduces the mean energy of the remaining molecules, therefore lowering the temperature of the liquid. When the vapour condenses back to a liquid or solid then the absorbed energy is released as sensible heat. The energy balance is calculated as:

$$R_n = G_1 + G_2 + H + \mathrm{AET}. \tag{2}$$

R_n can be measured with a radiation meter or calculated from a variety of methods as well (e.g. Bisht *et al.*, 2005), H can be measured with an instrument called a scintillometer (though it can be error prone, therefore a range of micrometeorological techniques are employed where available to measure H), G_1 can be measured with soil heat flux plates and G_2 can be measured through the surface temperature. Hence, AET can be calculated from the four known measurements. Like the water balance, it may be difficult to close the energy balance. In the energy balance equation, R_n may be considered an upper bound for AET, but the 'energy' here neglects the 'atmospheric energy' from dry air and windy conditions. If there is no R_n then there would be no AET according to this model, unless, for instance, H is negative, which can occur under some conditions (Baldocchi, 1992). Nonetheless, 'energy' in the form of a dry atmosphere can lead to AET under zero R_n (Fisher *et al.*, 2007). Similarly, if there is some R_n but the atmosphere is saturated (high humidity) with little wind, then AET would not occur at as high a rate as under windy, dry air conditions.

Temperature-based models

Mean air temperature (T_a) is one of the easiest climatic variables to measure and is linked to PET because T_a may vary with energy supply (and sensible heat). Xu & Singh (2001) reviewed seven T_a-based PET models (Thornthwaite, 1948; Blaney & Criddle, 1950; Hamon, 1961; Romanenko, 1961; Hargreaves, 1975; Linacre, 1977; Kharrufa, 1985), all of which include some empirical calibration. The most widely-used T_a-based model is from Thornthwaite (1948):

$$\mathrm{PET} = C\left(\frac{10T_a}{I}\right)^a \left(\frac{d}{12}\right)\left(\frac{N}{30}\right) \tag{3}$$

where C is 1.6, I is the yearly sum of $(T_a/5)^{1.514}$ for each month, d is the average number of daylight hours per day for each month, N is the number of days in the month, and the superscript a is $(6.75 \times 10^{-7} I^3) - (7.711 \times 10^{-7} I^2) + 0.01792I + 0.49239$. Most of the other T_a-based or Thornthwaite-type models follow a similar mathematical form based on T_a and some empirical constants. Thornthwaite-type models have one particular advantage over other T_a-based models for ecological application – the inclusion of daylight hours, which are implicitly related to R_n and the relative ability to photosynthesize. This equation was based primarily on data from the USA, and has since been modified and extended for various applications (e.g. Willmott *et al.*, 1985). T_a-based models may be inaccurate or wrong altogether, however, depending on where they are applied, for example in the tropics (Fisher *et al.*, 2009) and in areas such as deserts that do not meet the Thornthwaite assumption of vegetation cover (Thornthwaite & Mather, 1955). Thornthwaite suggested his method could be replaced by a more physically based method when the theory and suitable data become available (Thornthwaite, 1948). The Thornthwaite model is for PET only – there is no explicit indication of the water supply in the equation (but PET may equal AET under well-watered conditions).

Radiation-based models

Variability in R_n represents a major source of the variability in AET. Without knowing the exact partitioning of R_n, we can estimate only PET. Xu & Singh (2000) reviewed eight radiation-based PET models (Makkink, 1957; Turc, 1961; Jensen & Haise, 1963; McGuinness & Bordne, 1972; Priestley & Taylor, 1972; Hargreaves, 1975; Doorenbos & Pruitt, 1977; Abtew, 1996), although most of them use total solar, rather than net, radiation because the former data are more easily accessible than the latter. In fact, most radiation-based models also require T_a, so in essence should be referred to as radiation–temperature-based models, but we simplify the classification to 'radiation-based' to draw the difference between them and the temperature-only-based models. The most widely used radiation-based PET model, which relies on R_n, is from Priestley & Taylor (1972):

$$\mathrm{PET} = \alpha \frac{\Delta}{\Delta + \gamma} R_n \tag{4}$$

where α is 1.26 (for wet surfaces), γ is the psychrometric[4] constant, 0.066 kPa °C^{-1}, and Δ is the slope of the saturation-to-vapour pressure curve, $[17.502 \times 240.97 es(T_a)]/(T_a + 240.97)^2$, where $es(T_a)$, or saturation vapour pressure (the maximum vapour pressure the air can support at a given temperature), is $0.61121 \exp[17.502T_a/(T_a+240.97)]$. Priestley and Taylor originally applied their equation to oceanic and saturated land surfaces (no advection), and the equation largely reflects what is called 'equilibrium evaporation' or the evaporation from a wet surface into saturated air. This equilibrium connects energy at the surface to the air above it (called the convective boundary layer) so that AET, H, T_a and air humidity all balance around the α constant of 1.26 (Raupach, 2001). Most of the other radiation-based models follow a similar mathematical form based on

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energy too. Because it requires 2.45 MJ to vaporize 1 kg of water (at 20 °C), 1 kg of water is therefore equivalent to 2.45 MJ; 1 mm of water is thus equal to 2.45 MJ m^{-2}.

[3] The term 'latent heat of evaporation' was introduced by Joseph Black in the 1750s, but has since been replaced in thermochemistry by the term 'enthalpy of transformation'. The nomenclature for energetic AET is often λE or LE, but we keep AET here for simplicity.

[4] This relates changes in the partial pressure of water in air to changes in air temperature. It is associated with the 'psychrometer', or a hygrometer, which is used for measuring humidity.

radiation and some empirical constants. Radiation-based models, like the energy balance equation, have no explicit response to atmospheric demand separately from energy supply. Like the Thornthwaite model, the Priestley–Taylor model is for PET only.

Combination models

The most widely-used PET models fall within a class that combines energetic drivers such as R_n and T_a with atmospheric drivers such as vapour pressure deficit (VPD) and surface wind speed (u) – based on an equation developed by Penman (1948):

$$\mathrm{PET} = \frac{\Delta}{\Delta+\gamma} R_n + 2.6 \frac{\gamma}{\Delta+\gamma} \mathrm{VPD}\gamma\lambda\rho(1+0.54u). \tag{5}$$

where Δ and γ are as defined for the Priestley–Taylor model, λ is the latent heat of vaporization (*c.* 2448 MJ Mg^{-1}, depending on T_a) and ρ is air density (*c.* 1.234 kg m^{-3}, depending on T_a and pressure). VPD is equal to the amount of moisture the air can hold minus how much moisture is actually in the air; it is a function of relative humidity and T_a (and surface temperature, if available). The first part of the equation, equilibrium evaporation, is the same as the Priestley & Taylor (1972) radiation-based equation, but instead of multiplying it by an empirical coefficient (α), the equation extends to include the atmospheric components of VPD and u. The Penman equation was originally designed to eliminate the need for surface temperature data and to be parameterized with standard meteorological data; Penman tested the equation against open water, bare soil and turf. The equation is particularly sensitive to u and has no explicit vegetation component (Allen *et al.*, 1998; Fisher *et al.*, 2005). The Penman model is for PET only.

Monteith (1965) expanded the Penman (1948) equation to include not only energetic and atmospheric drivers but also the role of vegetation in controlling transpiration, particularly through the opening and closing of stomata. This expanded Penman equation, called the Penman–Monteith equation, includes the stomatal control as stomatal resistance (or, inversely, conductance, in the same units as precipitation, depth per time, usually m s^{-1} for conductance). When stomata are wide open, the stomatal resistance (r_s) term is small (i.e. similar to an open door; there is very little impedance from the stomata to water vapour exchange with the atmosphere); when stomata are closed, then r_s is large. The value of r_s changes throughout the course of a day. Scaling from leaf to canopy, r_s is taken as an average for the canopy and may include the soil hydraulic resistance as well, if not explicitly partitioned (Shuttleworth & Wallace, 1985, later explicitly partitioned the Penman–Monteith equation into evaporation from the soil and transpiration from the canopy). The Penman–Monteith equation includes one more resistance term – the aerodynamic resistance (r_a), which reflects the ease or difficulty with which it is possible to transfer water from the surface (right after it exits the stomata or soil) into the atmosphere. The value of r_a depends on and can be calculated from wind (i.e. u) for the transfer and the friction of the wind against the surface (which depends on how rough or smooth the surface is), and is related to VPD, which determines the strength of the gradient along which water vapour transfer occurs. The r_a term substitutes the part of the Penman equation that modifies VPD. Monteith also included the specific heat of water (c_p = 4.1855 J g^{-1} °C^{-1} at 15 °C and 101.325 kPa), which is the amount of heat energy that water can absorb until the temperature of 1 g of water is changed by 1 °C. The Penman–Monteith equation is:

$$\mathrm{AET} = \frac{\Delta R_n + c_p \rho \mathrm{VPD}/r_a}{\Delta + \gamma + \gamma(r_s/r_a)}. \tag{6}$$

The Penman–Monteith equation was originally designed for agriculture.[5] If used in a more diverse ecosystem, such as the tropical moist forest biome for example, it then becomes difficult to characterize r_s at the forest or ecosystem level because many different species in the same vertical profile have different light environments, rooting depths and leaf traits (Fisher *et al.*, 2009). Because the resistances are difficult to measure, the Penman–Monteith equation is difficult to parameterize (i.e. to find the data that the equation needs) and often incorporates introduced error by the unknown parameters (Raupach & Finnigan, 1988). However, if one considers r_s to be negligible (i.e. minimal over well-watered vegetation or zero over open water), then the Penman–Monteith equation can be used to estimate PET.

ET measurements

Pan evaporation

Perhaps the easiest method by which to measure evaporation is to take a pan of water, put it outside, and measure how much water remains after a day (assuming there is no precipitation into the pan or losses from leaks or animals). There are some standardized pan shapes and sizes, such as the Class A evaporation pan used in the USA, and the Symon's tank used in Europe, India and South Africa. Pan evaporation does not include transpiration, however, and is limited in that it is an artificial system (i.e. it has metal sides that get hot in the sun, it has different absorption characteristics from vegetation or soil and it has an oasis effect on T_a) that is supposed to represent a natural system (Ohmura & Wild, 2002; Roderick & Farquhar, 2002).

Sap flow

Sap flow systems are designed as probes inserted into the xylem of a plant that measure the rate at which water flows through the xylem (Čermák *et al.*, 1973; Granier, 1985). A heater probe may be vertically positioned between an 'up-stream' temperature sensor and 'down-stream' temperature sensor (Burgess *et al.*, 2001). A pulse of heat may be released into the transpiration stream and the time it takes that pulse of heat to reach the temperature sensor is the flow rate of the sap (length over time).

[5] The Penman–Monteith equation is the equation recommended by the Food and Agriculture Organization (FAO) of the United Nations (Allen *et al.*, 1998).

The sap flow, which is not a direct measure of evaporation of the entire canopy, may be scaled to whole plant/tree transpiration (with error introduced in scaling due to spatial and temporal representativeness), but it does not measure soil evaporation (Enquist *et al.*, 1998). Sap flow varies by species, but sapwood area (as well as tree age, height and other functional variables) accounts for the majority of the variation in tree water use (Baldocchi, 2005).

Lysimeters

A lysimeter is a balance underneath the soil, often in a tank or laboratory setting, that measures the change in weight from water loss (Howell *et al.*, 1991). It is very difficult to construct and operate an accurate lysimeter, which makes robust spatial sampling difficult, and often what is being measured does not represent the natural system accurately. Mini-lysimeters may be constructed as soil in a plastic collar that is easy to remove, weigh and return, but water flow may be influenced by the collar itself.

Eddy covariance

Evapotranspiring water vapour off the land surface combines with wind (moving in circular motions called eddies, like swirling water in a river) that transports the water vapour to the atmosphere. Instruments attached to towers extending above the canopy measure the water vapour concentration (via an infrared gas analyser) and the wind speed and direction (via a sonic anemometer) for large areas. The covariance of that water vapour with the vertical wind speed is calculated to give total AET for the given area. The measurements are recorded rapidly (data are generally provided as 30-min averages), continuously (assuming no equipment failures and, of course, funding) and with minimal disturbance to the site being measured. There are currently hundreds of eddy covariance towers world-wide providing data in a unified framework called FLUXNET (Baldocchi *et al.*, 2001; Baldocchi, 2008).

Other micrometeorological techniques include Bowen ratio systems, which are based on similar eddy diffusivity concepts and molecular diffusion as well as the energy balance equation, and, flux-gradient approaches, which are based on the relationship (Monin–Obukhov similarity theory) between vertical flow and a number of meteorological parameters (e.g. height, buoyancy, surface stress, virtual temperature, acceleration, pressure, momentum).

There are some limitations to these micrometeorological methods, however. The sites are restricted to flat terrain (so that the wind source is predictable) with consistent vegetation around the area (it is difficult to know where the AET is coming from if the vegetation is spatially heterogeneous). Because the method relies on vertical wind speed, errors are introduced when wind speed (turbulence) is low (especially at night) or when there is horizontal wind 'drainage' below the above-canopy sensors (Fisher *et al.*, 2007). The measurements at these sites generally include the components of the energy balance equation (equation 2), but are often in imbalance (Moncrieff *et al.*, 1996).

MATERIALS AND METHODS

There are more than 50 PET methods or models, but we compared across a range of sites the three most commonly used models, which are each in a different category of ET model: the Thornthwaite (1948) model is temperature based, the Priestley & Taylor (1972) model is radiation based, and the Penman–Monteith model (Monteith, 1965) is a combination equation. We constructed a latitudinal transect through the Americas – from northern Alaska to southern Brazil – using monthly meteorological data from 10 FLUXNET sites at 10 different International Geosphere–Biosphere Programme (IGBP) classes of land cover to test the three PET models. An eleventh site, in South Africa, was added to include an IGBP class that was not part of the FLUXNET sites in the Americas (Table 1). The data were collected in 2004 (two sites), 2003 (five sites), 2002 (two sites), 2001 (one site) and 1999 (one site). Data included: R_n (W m^{-2}), T_a (°C), VPD (kPa) and u (m s^{-1}).

We also compared the Thornthwaite, Priestley–Taylor, and Penman–Monteith models with each other continentally and globally using gridded 0.5° monthly data from the ISLSCP-II archive (Los *et al.*, 2000; Hall *et al.*, 2005). The data (year 1990) include: radiation data based on measurements from the Goddard Earth Observing System version 1 (GEOS-1) reanalysis datasets (Schubert *et al.*, 1993), cloud parameters and surface albedos from the International Satellite Cloud Climatology Project (Pinker & Laszlo, 1992; Rossow *et al.*, 1996), normalized difference vegetation index (NDVI) (Los *et al.*, 2000) and climate data from the Climate Research Unit (CRU) (New *et al.*, 2000).

RESULTS

PET for different land cover types across a latitudinal transect

Do different PET models produce equivalent PET estimates? The answer will vary depending on the spatial and temporal scales, as well as the land cover. For example, the three PET models (Thornthwaite, Priestley–Taylor and Penman–Monteith) that we compared at the 11 sites performed similarly at some sites, but diverged greatly at the majority of the sites (Fig. 1). Generally, the models differed from each other in average annual PET by more than 25%. For instance, the Thornthwaite and Penman–Monteith models differed by 1% at the permanent wetland site and 6% at the closed shrubland site. But the Thornthwaite model almost always estimated smaller values of PET than did the Priestley–Taylor (80% across all sites) and Penman–Monteith (71% across all sites) models. This difference suggests that either the Priestley–Taylor and Penman–Monteith models are over-estimating, or that there may be more PET occurring than estimated by the Thornthwaite model, which is dependent on temperature and day length alone, due to other factors such as atmospheric control. The Penman–Monteith model often gave the highest estimates (22% higher than the Priestley–Taylor model across all sites).

Table 1 Description of sites used in this analysis in order from north to south.

Site	IGBP land-cover type	Latitude	Longitude	Mean annual precipitation (mm)	Mean annual air temperature (°C)	Reference
Barrow	Permanent wetland	71.323	−156.626	86	−12.8	Vourlitis & Oechel (1999)
Bonanza Creek	Open shrubland	63.923	−145.744	249	−0.3	Zhuang *et al.* (2003)
Sask.-SSA Old Aspen	Deciduous broadleaf forest	56.629	−106.198	429	0.3	Amiro *et al.* (2003)
Western peatland, Labiche	Mixed forest	54.954	−112.467	461	1.1	Glenn *et al.* (2006)
Lost Creek	Closed shrubland	46.083	−89.979	828	4.1	MacKay *et al.* (2007)
Niwot Ridge	Evergreen needleleaf forest	40.033	−105.546	595	0.4	Monson *et al.* (2002)
ARM Southern Great Plains site, Lamont	Cropland	36.605	−97.488	843	14.8	Fischer *et al.* (2007)
Manaus KM34	Evergreen broadleaf forest	−2.609	−60.209	2252	26.7	Araújo *et al.* (2002)
Fazenda Nossa Senhora	Grassland	−10.762	−62.357	1664	23.9	von Randow *et al.* (2004)
Reserva Pe-de-Gigante	Woody savanna	−21.620	−47.650	1420	20.9	da Rocha *et al.* (2004)
Skukuza, Kruger National Park	Savanna	−25.020	31.497	622	20.3	Scholes *et al.* (2001)

IGBP, International Geosphere-Biosphere Programme.

Site	Year	Dominant species
Barrow	2002	*Carex aquatilis, Dupontia fischeri, Arctophila fulva*
Bonanza Creek	2003	*Festuca altaica* and deciduous shrubs
Western peatland, Labiche	2004	*Picea mariana, Larix* spp., *Betula, Ledum, Sphagnum* spp., *Aulocomnium* spp., *Tomentypnum* spp., *Drepanocladus* spp.
Sask.-SSA Old Aspen	2003	83-year-old mature *Populus tremula* with a few balsam poplar, thick *Corylus* understorey
Lost Creek	2003	Shrub wetland; *Alnus incana, Salix* spp.
Niwot Ridge	2003	*Abies lasiocarpa, Picea engelmannii, Pinus contorta*
ARM Southern Great Plains site, Lamont	2003	*Triticum aestivum*
Manaus KM34	2004	Old-growth closed-canopy terra firme (non-flooded) forest. > 150 tree species per hectare.
Fazenda Nossa Senhora	1999	*Brachiaria brizantha*
Reserva Pe-de-Gigante	2002	Over 25 species from families Anacardiaceae, Annonaceae, Asteraceae, Bignoniaceae, Caryocaraceae, Erythroxylaceae, Fabaceae, Malpighiaceae, Melastomataceae, Myrtaceae, Ochnaceae, Polygalaceae, Sapindaceae, Sapotaceae, and Smilacaceae
Skukuza, Kruger National Park	2001	Broad-leafed *Combretum* savanna and fine-leafed knob-thorn savanna

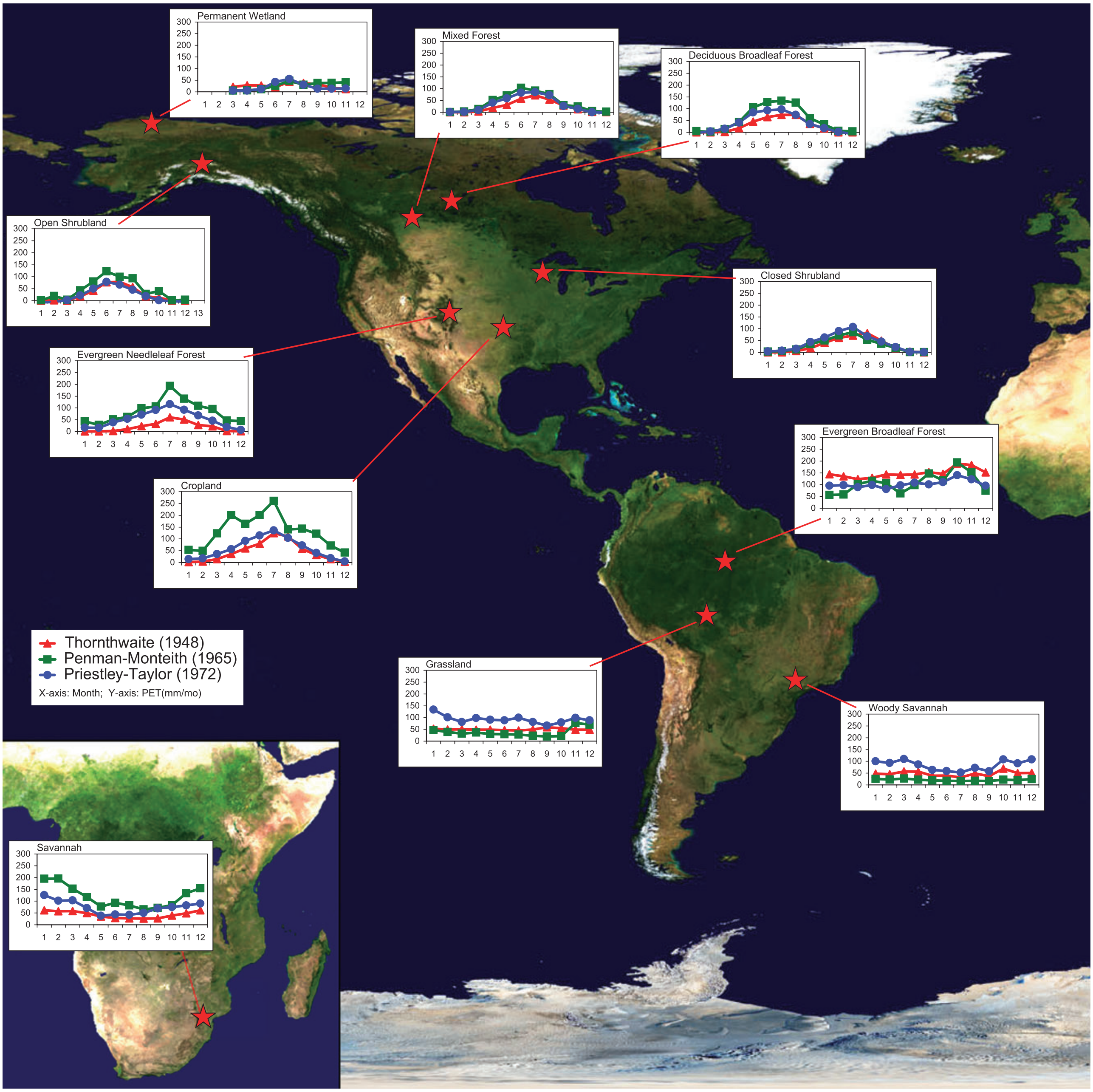


Figure 1 Predictions of monthly potential evapotranspiration (mm month^{-1}) based on three models – Thornthwaite (1948), Priestley & Taylor (1972) and Penman–Monteith (Monteith, 1965) – at 11 FLUXNET sites with different land-cover classes over the course of a year. See Table 1 for site descriptions. [Correction added on 23 August 2010, after first online publication: mislabelling errors to the key of Fig. 1 are corrected, including the transposition of the Thornthwaite and Priestley–Taylor labels.]

The overall average PET for each model at each site is important, but so too are the temporal dynamics throughout the course of the year (e.g. O'Brien, 1993, 1998; O'Brien *et al.*, 1998, 2000). Each model responds to its respective input parameters and drivers, which is the cause of temporal model variation. Most of the inputs covary with one another; for example, T_a tends to increase with increasing R_n. In this case, results from a temperature-based model and a radiation-based model may look similar to each other. When the meteorological inputs break from the expected covariance, however, then the model outputs also become more distinct.

Although the individual FLUXNET sites in our analysis contained different land-cover classes and were separated along a latitudinal transect, the sites were not each entirely distinctive because, for example, sites near to one another had some similarities in climate. In choosing the sites, we took no account of differences in soil type, nutrient status or land-use history, meaning that there are factors other than climate involved in the comparison. Notwithstanding, our analyses demonstrate differences in PET that to a large degree relate to land-cover type and general climatic conditions: both matters of importance to macroecologists and biogeographers (Currie, 1991; O'Brien, 1993,

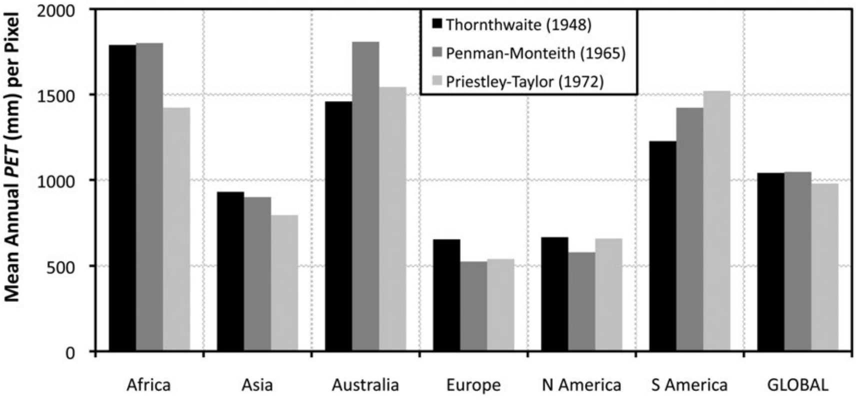


Figure 2 Continental and global mean annual potential evapotranspiration (PET) per pixel (0.5°) estimates for three PET models (Thornthwaite, 1948; Monteith, 1965; Priestley & Taylor, 1972) using ISLSCP-II data for 1990.

1998, 2006). In some cases, the different PET models produced similar estimates (as time series and/or as annual averages or sums), but not in general. These findings therefore exemplify how the choice in PET model may influence the estimate in PET across a range of sites incorporating a large gradient in environment and land-cover type.

Continental and global patterns of PET

There may be differences in model estimations at sites with different land-cover classes, but how do the models compare when land-cover information is aggregated, as in regional, continental or global analyses? When we calculated a per pixel average of the annual sum of PET for each continent, it would seem that there is relatively little variation between the models and no consistent rank order of values (Fig. 2). In North America, the Thornthwaite and Priestley–Taylor models differ by 7 mm (mean annual PET per pixel); in Africa, the Thornthwaite and Penman–Monteith models differ by 11 mm; and in Europe the Priestley–Taylor and Penman–Monteith models differ by 15 mm. In Asia, Australia and South America, however, the models exhibit greater divergence. The models are all very similar in global average – the Penman–Monteith and Thornthwaite models differ by only 6 mm.

However, examination of the global maps (Fig. 3a–c) reveals high variability in spatial pattern. It is evident that there is wide variability across any east/west line (or band) of latitude. Although the mean values for the Thornthwaite and Penman–Monteith models were similar for Africa (Fig. 2), the distribution of values for the Thornthwaite model was much wider than for the Penman–Monteith model.

In some areas the models closely agree with each other, whereas in other areas the models deviate greatly (Fig. 4a–c). The Priestley–Taylor and Penman–Monteith maps are the most similar of the three models because radiation tends to be the dominant control over PET globally relative to air temperature, wind speed, vapour pressure deficit, stomatal resistance and aerodynamic resistance. Where the two models disagree most is for areas with low vegetation cover (i.e. NDVI), primarily in deserts. The Penman–Monteith model tends to estimate even greater PET relative to the Priestley–Taylor model for these areas. The Priestley–Taylor model tends to estimate greater PET in areas of high vegetation cover throughout the pan-tropics (Fig. 4a).

The Thornthwaite model departs from the Priestley–Taylor and Penman–Monteith models for most areas (Fig. 4b, c). In the scatterplots an exponential relationship illustrates the linkages between the Thornthwaite model and both the Priestley–Taylor and Penman–Monteith models: the Thornthwaite model is primarily driven by T_a, but the Priestley–Taylor and Penman–Monteith models, whilst predominantly driven by R_n, also include T_a as an exponential function in their equations (Δ, see equation 4). With respect to the 1:1 line (where the two models would equal each other), the Thornthwaite model differs most from the other two models at the lowest values of PET (0–500 mm) under low vegetation cover and at a mid-level range (1000–1500 mm). The Thornthwaite model estimates much greater values of PET in the high northern latitudes, but also in the Sahara, Middle East, India and parts of Australia, and much lower values for most of the rest of the world.

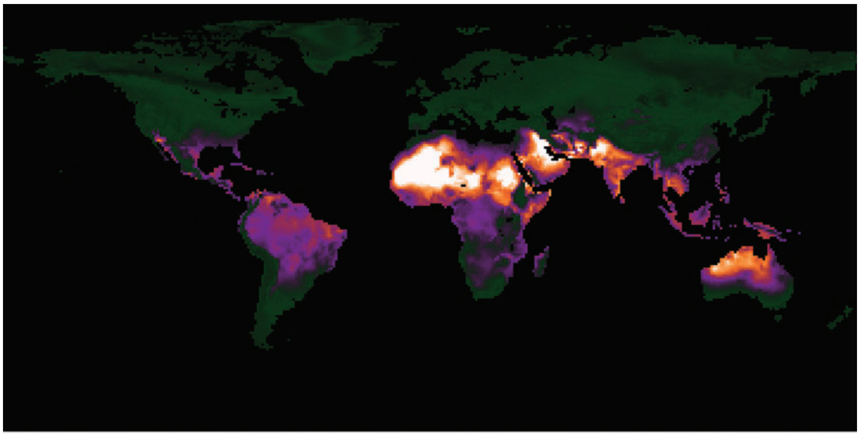
DISCUSSION

From equations to maps

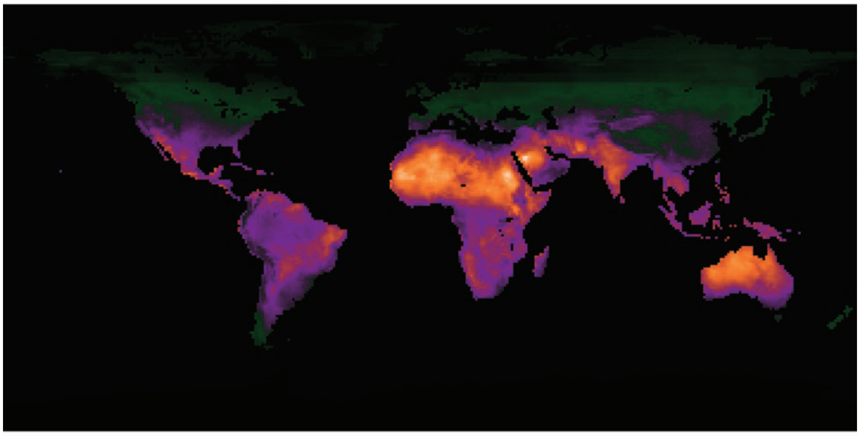
It should be clear from the Results that the choice of PET model can significantly alter the PET estimate. Further, it should be clear from the Materials and Methods that the PET models differ in what environmental parameters govern them. How then do we connect what we see in equation form in the methods to the patterns shown in the results? Exactly why are there different estimates and patterns in the results? Moreover, how do these differences matter to geographical ecology?

First, the results are similar to other studies that compared PET equations against data. For example, Hulme *et al.* (1996) showed that PET for Africa for the Thornthwaite model was generally lower than that for the Penman and Priestley–Taylor models, except for near the equator. Similarly, Vörösmarty *et al.* (1998) showed that PET estimated for the USA using the Thornthwaite model was lowest (see also McKenney & Rosenberg, 1993; Lu *et al.*, 2005), except for the Arizona desert where Priestley–Taylor provided the lowest values (see also Federer *et al.*, 1996), and the north where Penman–Monteith provided

a) Thornthwaite (1948)



b) Penman-Monteith (1965)



c) Priestley-Taylor (1972)

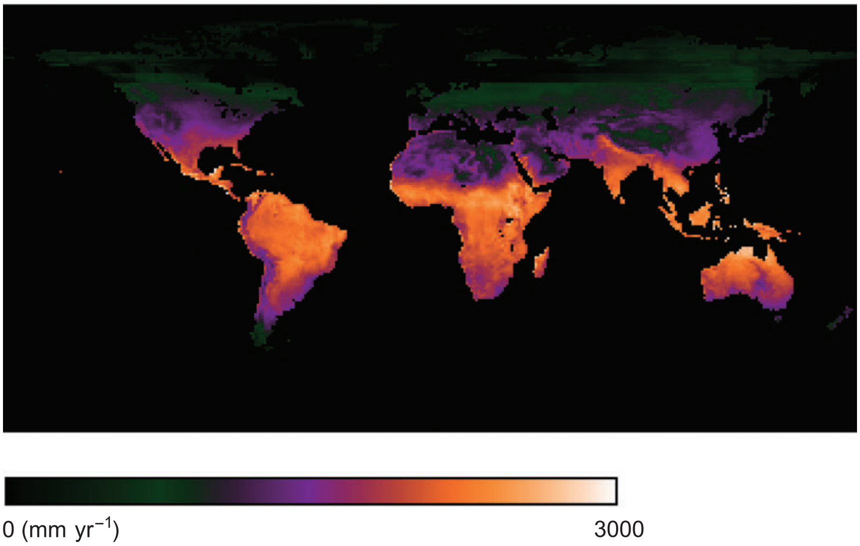
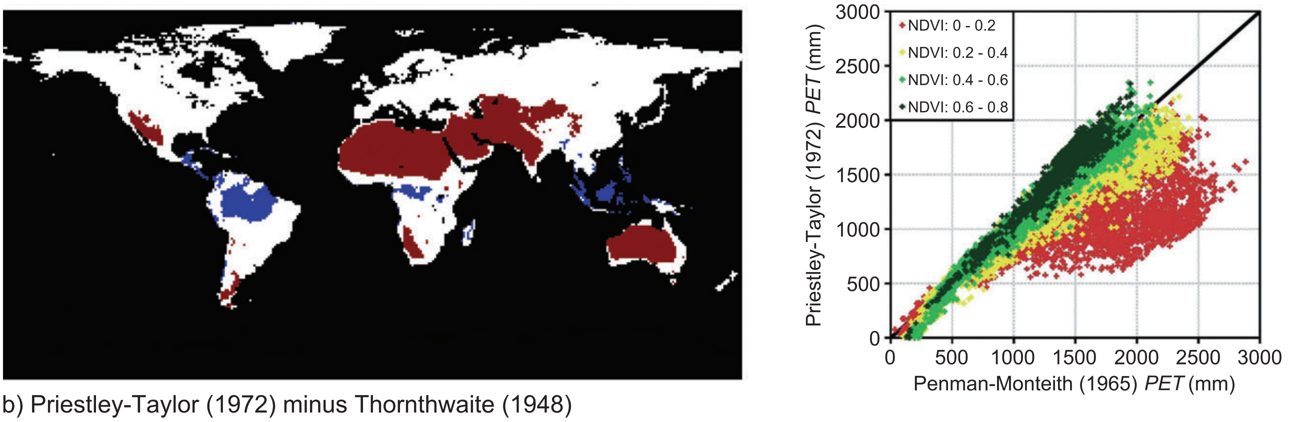


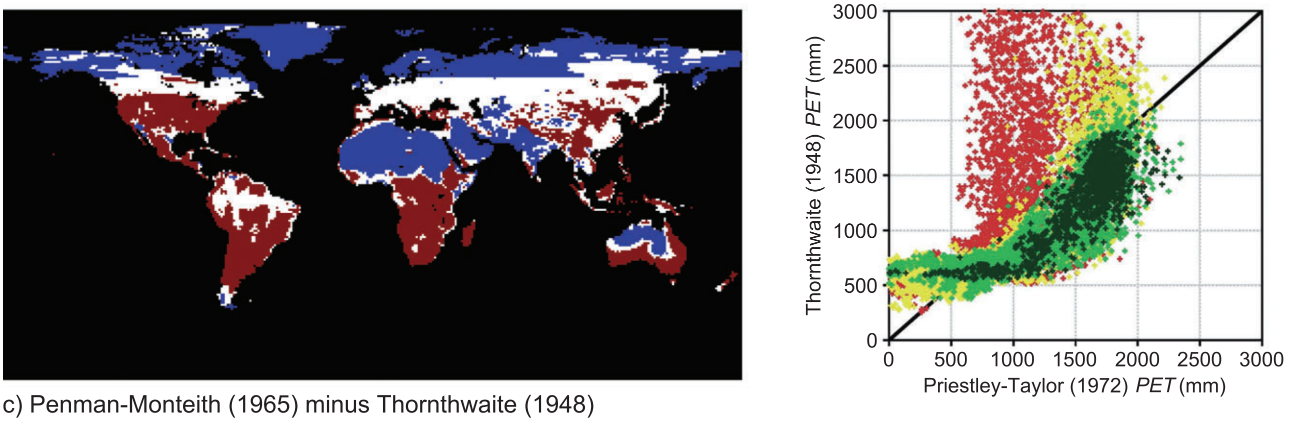
Figure 3 Mean annual potential evapotranspiration (models driven with 0.5° ISLSCP-II data for 1990) for (a) the Thornthwaite (1948) model, (b) the Penman–Monteith (Monteith, 1965) model, and (c) the Priestley & Taylor (1972) model. Although the entire land surface is represented, not all models are appropriate everywhere, i.e. Thornthwaite-type models assume vegetative cover.

the lowest values. For our results, values from Thornthwaite's PET were generally > 150 mm lower than those of Priestley–Taylor or Penman–Monteith for the USA and sub-Saharan Africa (shown as the > 150 mm difference between the models in Fig. 4). We also observe a similar pattern to those reported by Vörösmarty *et al.* (1998) and Federer *et al.* (1996) for the Arizona desert using the Priestley–Taylor model, except in northern Arizona.

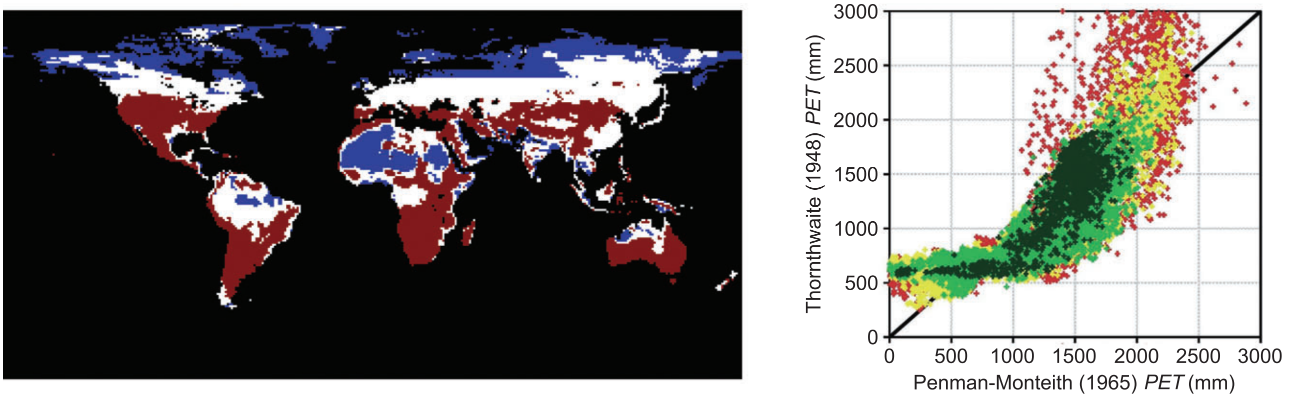
a) Penman-Monteith (1965) minus Priestley-Taylor (1972)



b) Priestley-Taylor (1972) minus Thornthwaite (1948)



c) Penman-Monteith (1965) minus Thornthwaite (1948)



Blue: Difference < -150 mm Red: Difference > 150 mm

Figure 4 Differences in mean annual potential evapotranspiration (mm) estimates (models driven with ISLSCP-II data for 1990) between (a) the Priestley & Taylor (1972) and Penman–Monteith (Monteith, 1965) models, (b) the Priestley & Taylor (1972) and Thornthwaite (1948) models, and (c) the Penman–Monteith (Monteith, 1965) and Thornthwaite (1948) models. The scatterplots are coloured by normalized difference vegetation index (NDVI; i.e. vegetation cover), the value of which ranges between 0 and 1 (the maximum average NDVI for 1990 was 0.8).

In contrast, Mintz & Walker (1993) found that the Thornthwaite estimates were in good agreement with those based on the Priestley–Taylor and Penman–Monteith models. Upon further inspection, however, it should be noted that they made this comparison at only four sites, which is easily overlooked in their globally focused/titled paper. Three of the four sites were located in the mid-latitudes (41–48° N) and the fourth was in central Africa. Nonetheless, our results agree with theirs for these areas, which happen to be among the limited locations globally that the Thornthwaite model agrees well with the Priestley–Taylor and Penman-Monteith estimates: a mid-latitudinal band crossing Canada, Europe and Asia, as well as Central Africa (Fig. 4); this pattern also holds for the mid-latitude cropland site in our site-level analysis (Fig. 1).

In general, however, the Thornthwaite estimates do not agree well with the Priestley–Taylor and Penman–Monteith estimates globally (Fig. 4), while the latter agree well with one another except in the deserts and the tropics. The explanation of why the Priestley–Taylor model gives PET estimates in the tropics more than 150 mm greater than the Penman–Monteith model is because R_n is so high in the tropics, but VPD is relatively low due to the high humidity, thus the Penman–Monteith model suppresses the PET from that of Priestley–Taylor, which does not include VPD. The Thornthwaite model diverges from the others greatly when there is low vegetation cover, which would be expected because the Thornthwaite model assumes vegetation cover.

At the site level, differences in PET estimates from different models arise when environmental parameters such as T_a, R_n, VPD and u vary more or less together. For example, if T_a and R_n correlate well with one another (e.g. $r^2 = 0.52$ for the closed shrubland in Fig. 1), then the Thornthwaite and Priestley–Taylor models are likely to agree well with each other. Where those environmental parameters do not correlate well (i.e. $r^2 = 0.09$ for the grassland in Fig. 1) those two models are not likely to agree well with each other. Similarly, the Penman–Monteith estimate agrees well with Priestley–Taylor at the mixed forest site, for example, and VPD and R_n also correlate reasonably well at that site ($r^2 = 0.63$). At the cropland site, however, the Penman–Monteith estimate does not agree well with the Priestley–Taylor estimate, and the correlation between VPD and R_n is much lower ($r^2 = 0.39$) than that at the mixed forest site.

These sometimes very large differences in PET estimates have huge implications for their use in geographical ecology. Too much energy (e.g. high temperatures, water demand, PET) is stressful and limiting to plants (and animals). It is therefore important that PET metrics are capable of accurately capturing this facet of energy regimes. The Penman–Monteith model is more physically based than the other models because it also reflects the atmospheric demand component of the energy regime, which the other models do not. However, plants may close their stomata when VPD is high, thus the VPD-insensitivity of Priestley–Taylor may actually make Priestley–Taylor a better indicator of PET that is more consistent with and relevant to plant function. Nonetheless, Penman–Monteith may be better for indicating stressful climates. This is also why we should expect, on theoretical grounds, to see a humped (Gaussian) relationship between energy supply and photosynthesis and subsequent biological activity across a full range of energy regimes globally (O'Brien, 1998, 2006; Field *et al.*, 2005).

Seasonality is another key facet of climate regimes that may be hugely informative ecologically (Boyce, 1979; Phillips *et al.*, 1994; Hurlbert & Haskell, 2003). All the key climate variables can be summed or averaged to annual values, or to seasons of the year, or indeed monthly data can be used. Thus, making use of an array of annual and sub-annual data series, such as the hottest and coldest months, or the driest and wettest periods, allows increased flexibility in building explanatory models of species distributions, species richness or other emergent patterns such as major ecosystem types. The importance of this is that users should aim to understand the properties of the PET metric selected and to decide not just on grounds of accuracy and precision in climatological terms but also to consider the suitability in terms of the ecological hypotheses being examined.

Uncertainty and scale

Potential sources of error in PET estimates could come from the model itself and/or uncertainty in the input data. First, if we assume perfect input data then how do we know if the PET model is accurate? There is no true measure of this theoretical property with which to validate the model estimates. Pan evaporation is an approximation of PET, but is subject to the biases and assumptions described previously, and it does not include plant transpiration. One could compare measured AET at the FLUXNET sites with modelled PET under well-watered conditions and determine if the two match equally. If AET exceeds PET then we know that the PET estimate was too low, and if AET is less than PET then we may expect that the PET estimate was too high. There are no perfect AET measurements under optimal conditions, but the FLUXNET database (i.e. Fig. 1) may provide a portion of these measurements at similar sites under well-watered conditions for at least part of the year, and with a quantification of the error in the measurements (Moncrieff *et al.*, 1996).

What does uncertainty in the input data mean for uncertainty in the model estimate? There are a number of different methods with which one can calculate the propagation of input error through a model (e.g. Gaussian error propagation, maximum likelihood, method of moments, Monte Carlo methods). The sensitivity of the model to each input parameter is critical in determining how important it is to have high accuracy across all inputs, or just among the key drivers (Fisher *et al.*, 2005; Medlyn *et al.*, 2005). Further, the range within which the input parameter fluctuates is also important – if the model is very sensitive to a given parameter, but that parameter does not fluctuate widely, then a noticeable difference in the model output is unlikely to be seen. Finally, there is the possibility that the input data are entirely wrong (and unrealistic), but in the right combination the model output could still appear realistic. Essentially, different parameter estimates in the same model could lead to similar results (Medlyn *et al.*, 2005). Although it is generally agreed that there is a wide range of uncertainty and validation tests that will help the model user understand the limitations in the model and model outputs, there is no standard approach to doing this (Rykiel, 1996).

In practice, some authors, aware of some of the problems and pitfalls of using interpolated and modelled climate data opt to use data derived directly from long-term records from fixed climate stations (e.g. O'Brien, 1993, 1998; Field *et al.*, 2005), whilst many others have based their analyses on interpolated datasets such as WorldClim (e.g. Peterson & Nakazawa, 2008). The strength of the former approach is that the data are both precise and accurate, but the limitation is that they apply only to a particular location and are data often needed to characterize much larger regions. By contrast, coarse-scale, interpolated climate datasets provide far more complete spatial coverage at the cost of accuracy and potentially of introducing unknown systematic bias (e.g. adjusting to sea level when averaging over varying topography).

How does the prediction vary with changing spatial resolution (i.e. from 1 km^2 to 100 km^2 to 1° and 10° grid cells)? The choice (and associated error) of spatial resolution depends on the scale of examination – is the study of a forest, a region, the globe? If the study is of a forest in a fragmented landscape, one would not want to use data from a spatial scale that is so large as to include mostly non-forest (Turner *et al.*, 2003). The temperature in a clear-cut is different from that in the forest, so to run a model using an averaged temperature from both sites would not represent the forest well. Similarly, if the study is of the whole landscape, then it is acceptable to include data that combine and average the forest fragments, but not acceptable to evaluate the whole landscape using only forest data. The sensitivity of the model to different input parameters may change with spatial scale. For example, at the scale of a leaf, a small breeze may substantially affect the transpiration of water through the leaf stomata; but at the scale of a forest, that small breeze would be insignificant relative to the overall radiation input from the sun. Thus, ET (PET and AET) is more or less connected – or coupled – to environmental controls, depending on the spatial scale (Jarvis & McNaughton, 1986).

How does the prediction of ET vary with changing temporal resolution (i.e. from seconds to minutes, hours, days, months and years)? The choice of temporal resolution depends on the scale on which the unit of analysis changes. There are climatic shifts (ice ages and warming), year-to-year differences associated with decadal events (i.e. El Niño) or large-scale disturbances (e.g. eruption of Mount Pinatubo) and within-year seasonal changes. ET varies much more within the course of a day relative to variation from the daily average from one day to the next. It is difficult and error-prone to calculate ET for a given hour from daily averaged information; for instance, the average daily temperature is much warmer than the temperature in the morning. Conversely, it is also difficult to calculate ET for a given day from a single measurement during the day – in fact, this is the subject of much research as the diurnal cycle of ET (generally focused on AET) from remote sensing is typically estimated from one or two satellite overpasses per day (Crago, 1996). Therefore using one time-scale as representative of another time-scale may introduce new sources of error into the estimates.

GUIDE TO CHOOSING AN ET MODEL

From examination of the literature on species diversity gradients cited herein, it is rarely the case that authors provide a clear argument for their choice of ET (or other climatic) data. To some extent we surmise that research teams frequently choose data on the basis of the ease of availability. With so many ET models to choose from, how should one select the model and data that will be the most appropriate to the task in hand?

There are two simultaneous and potentially contradicting goals when choosing a model (Raupach & Finnigan, 1988): (1) accurate prediction and (2) simplicity (ease of use). The most accurate model may be the most complex model, but this assumes that the input data are completely available and accurate; also, the complexities of such models may not be very important – in other words, ET at a specific study site may be sensitive to only a few of the many potential controlling factors. Above all, the model must be appropriate for the study system. Therefore, two critical factors must be assessed in choosing a model: (1) the quality and availability of the input data, and (2) the sensitivity or degree of response of ET to the potential controls for the geographical area of the study system.

The first step is to determine how simple or complex a model is needed, then to assess the data required to run the model for the spatial and temporal resolutions required. The data should reflect the spatial and temporal resolution of the study in question. If the data are inappropriate (e.g. measuring ET at the peak of a mountain using data only from the base of the mountain), then the question must be reformulated or rephrased.

First, define the climate regime of the study area; this will define the class (temperature based, radiation based or combination) of PET model to use (which will be the basis of an AET model if so needed). Is the climate arctic, boreal, dry (arid and semi-arid), subtropical/Mediterranean, temperate, temperate–continental (with hot/warm summers) or tropical? In general, a temperature-based model should be avoided if data are available to run the other models or if vegetation cover is low. Nonetheless, a temperature-based model may be applicable in the mid-latitudinal temperate regions, where it has been shown to agree well with radiation-based and combination models. Both the radiation-based and combination models can be used in all other climates. In the tropics, however, it should be noted that a combination model will probably give lower PET estimates than will a radiation-based model. If the study is of global extent then a single model should be chosen based on other criteria.

The next step is to define the land cover and vegetation type. A literature search could reveal a model specifically designed for that land-cover type (e.g. specific agricultural crops). Otherwise, the 'default' PET model may be used to match the PET model class: Thornthwaite (1948) for temperature-based, Priestley & Taylor (1972) for radiation-based and Penman–Monteith (Monteith, 1965) for a combination model.

Next, define the spatial and temporal resolutions of the study. Then, determine the input data and availability. At this stage, it should be defined whether the interest is in energetic demand (PET) or water flux (AET). It may be that a combination model was chosen, for example, but only data for a temperature-based model are available. The original question would subsequently need to be revisited to determine what level of accuracy is required from the PET estimate.

The final step in choosing an ET model is to calculate the error or uncertainty associated with the ET estimate. The steps and details of this process can be found in Table 2 (Guide to choosing an ET model for geographical ecology).

CONCLUSION

How might current estimates of biodiversity change with different models? We have illustrated that the choice of PET model

Table 2 Guide to choosing an ET model for geographical ecology.

1. Define the climate regime, select the class of PET model (temperature-based, radiation-based, combination). Results from radiation-based or combination models are more theoretically robust than those from temperature-based models, but more difficult to parameterize.

Climate	PET model class
(A) Arctic	Combination or radiation-based
(B) Boreal	Combination or radiation-based
(C) Dry (arid and semi-arid)	Combination or radiation-based
(D) Subtropical/Mediterranean	Any
(E) Temperate	Any
(F) Temperate–continental (with hot/warm summers)	Any
(G) Tropical	Combination or radiation-based

2. Define land cover and vegetation type. Conduct literature search – there are more than 50 ET models to choose from. Numerous ET models have been developed empirically for specific land-cover types (especially agricultural). If no vegetation, then a Thornthwaite-type model may be in error. If in doubt, choose the 'default' PET model for the model class selected in step 1.

PET model class	'Default' PET model
(A) Temperature-based	Thornthwaite, (1948)
(B) Radiation-based	Priestley & Taylor, (1972)
(C) Combination	Penman-Monteith, (Monteith, 1965)

3. Define the spatial and temporal resolutions of the study.

4. Determine the availability and quality of input data (accuracy, precision and continuity). Is the interest in the energetic demands (choose PET) of a system or the water flux (choose AET, i.e. Fisher *et al*., 2008)? An AET model will require more input drivers than a PET model, especially with respect to soil moisture status. Do the data match the spatial and temporal resolutions of the study? If not, then what data remain, and do they match the input requirements for the selected model? If not, then may need to select new model or accept greater uncertainty or error in ET estimates. Check for:

Aerodynamic resistance above the canopy
Aerodynamic resistance between substrate and canopy
Air temperature
Boundary layer resistance
Fractional canopy cover
Leaf area index
Radiation (net, total; partitioned to canopy versus soil)
Relative humidity
Remotely sensed vegetation indices (NDVI, EVI, NDWI)
Root properties
Soil moisture
Stomatal resistance
Surface resistance of the substrate
Tree height
Vapour pressure deficit
Wind speed

5. Calculate the error or uncertainty with the ET estimate. Some options include:

Akaike information criterion
Bootstrapping
Gaussian error propagation
Maximum likelihood
Method of moments
Model efficiency
Monte Carlo methods
Normalized mean average error
Root mean square error
Standard deviation or error

Summary:

Climate/vegetation → Model class → Literature review → Model selection → Data review → Model confirmation → Model run → Uncertainty estimation.

ET, evapotranspiration; AET, actual evapotranspiration; PET, potential evapotranspiration; NDVI, normalized difference vegetation index; EVI, enhanced vegetation index; NDWI, normalized difference water index.

may significantly alter the estimate of PET, but generally PET is only one of several other environmental variables used within large multiple regression analyses describing (and occasionally predicting) spatial patterns in species richness (see 'Evapotranspiration in the ecological literature'). Therefore one can assume that the choice of PET model will also alter the structure of the model, the comparability of the analyses and, where prediction is attempted, the biodiversity estimate. The important question here may not be what the absolute estimate of biodiversity or PET is, but what the uncertainty or error is associated with different PET metrics and their associated environmental drivers. Confidence levels around our estimates of biodiversity may be derived from quantifying the propagation of these errors through the larger model. Certainly, different PET metrics vary from one another geographically, but models that are adopted by different authors using different PET metrics are not precisely comparable because some part of the variance in model outcomes and findings from papers using these metrics may be attributable to the use of different PET (as well as AET) metrics (see 'Evapotranspiration in the ecological literature'). One cannot compare someone else's model in any direct sense unless both parties are using the same metric or one that has been shown to have a consistent relationship with the other person's model.

In the present work we have presented a basic overview of the concepts, models and measurements of evapotranspiration (ET) in the context of macroecology and biogeography. We have demonstrated how different types of ET models vary more or less depending on spatial and temporal scales, as well as with geography, climate and land cover; and have argued that accuracy in the input data is directly linked with accuracy in the model output. We hope that our 'Guide to choosing an ET model for geographical ecology' (Table 2) will be useful to macroecologists and biogeographers requiring ET estimates for their studies.

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