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RESEARCH LETTER

Where on Earth are the "tropics"?

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Abstract. The tropics have long been a focal point of interest in ecology and evolutionary biology - but where actually are the tropics? Classically, the tropics have been defined as all areas lying between 23.4° North and South as these zones receive direct overhead solar radiation at some point during the year. However, a suite of different environmental and climatic characteristics have also been employed to classify regions as tropical or not. The aims of this paper are to 1) briefly review some of the different criteria commonly used to define the tropics, 2) map the extent and distribution of tropical land areas according to these different criteria, and 3) asses the concordance between these criteria and a sample of recent "tropical" studies. More specifically, we review eight criteria that are frequently used (implicitly or explicitly) to define the tropics. We then map the location and extent of land areas that are "definitely tropical" (i.e., the core tropics) and areas that are "tropical by most definitions". Finally, we examine how the different classifications apply to tropical research through an analysis of the study locations of >200 recent tropical biology articles. Depending on the definition, the extent of the terrestrial tropics ranges from 23 million to 66 million km^2 – a nearly threefold difference. Likewise, the classification of many areas as being tropical vs. non-tropical depends on the specific criterion employed. Of the tropical studies reviewed here, only 44% were based on data collected from the core tropics, and 12% of tropical studies were based on data collected from sites outside of the geographic tropics but with tropical climates. Many different criteria are used to classify areas as tropical vs. non-tropical, leading to inconsistencies when estimating the extent of tropical areas and variation in the classification of ecosystems and species as being tropical vs. non-tropical.

Keywords: biogeography, biotemperature, climate, Holdridge life zones, latitude, subtropics, tropical ecology.

Introduction

Biogeographers and ecologists often implicitly or explicitly classify areas, ecosystems, and/or species as being tropical vs. temperate (or non-tropical). This delineation of the Earth's tropical vs. temperate regions has provided an important spatially-explicit framework for many basic and applied hypotheses of historical and ecological biogeography, evolutionary biology and systematics (Wallace 1876, Wallace 1878, Futuyma 1998, Jablonski et al. 2006, Jansson et.al. 2013, Morrone 2013). Furthermore, the delineation of the Earth's ecosystems is integral to effective conservation planning (Lomolino et al. 2010, Ladle and Whittaker 2011, Feeley et al. 2017). Surprisingly, the criteria used to delineate the tropics from the non-tropics are usually not well-defined (but see Corlett 2013) and can differ greatly between studies.

Here, we briefly review eight of the most common criteria that have been used to define the tropics in ecological and evolutionary studies (Table 1). Using publicly-available data on solar radiation, climate (temperature and precipitation) and elevation, we map the tropics according to each criterion. We analyze the differences in the extent and the location of tropical land areas as defined under each criterion, and present maps of areas that are "definitively tropical" (i.e., meeting all criteria) or that are "tropical by most definitions" (i.e., meeting the majority of criteria). We then look at how the locations of more than 200 recent tropical studies (locations extracted from articles published in 2014, 2015, and 2016 in the journals *Biotropica* and the *Journal of Tropical Ecology* - both of which focus explicitly on studies of tropical species and systems) relate to the various definitions of tropical areas. For the purpose of this review, we focus exclusively on terrestrial systems, but it should be noted that many of the same definitions and criteria could also be applied to marine systems.

Table 1. Summary of eight criteria used to define the terrestrial tropics

Criterion	Brief description of tropics according to criterion
C1	Areas that receive direct overhead solar radiation
C2	Areas with a net positive energy balance
C3	Areas where mean annual temperatures do not vary with latitude
C4	Areas where temperatures do not go below freezing in a typical year
C5	Areas where the mean monthly temperatures are never <18°C
C6	Areas where the mean annual "biotemperature" ≥24°C
C7	Areas where the annual range of temperature is less than the average daily temperature range
C8	Areas where seasonality of precipitation exceeds seasonality of temperature

Methods and results

Defining and mapping the tropics

Criterion 1: All areas of the Earth's surface that receive direct overhead solar radiation at some time during the year

Given the current tilt of the Earth's axis, Criterion 1 corresponds to all areas between 23.4°S and 23.4°N - the tropics of Capricorn and Cancer, respectively (Berger 1976). This criterion does not incorporate any information about regional climate or energy balance. As such, many biomes and ecoregions are classified as being tropical under this criterion despite marked differences in their climates. To map the extent of the tropics under Criterion 1, we classified and tallied land areas as being tropical (absolute latitude ≤23.4°) at a 2.5-arc-minute resolution (approximately 5-km spatial resolution at the equator). Under Criterion 1, a total 50.191×10^6 km^2 of land is classified as tropical and 100.009×10^6 km^2 is classified as non-tropical; in other words, 33.4% of the Earth's land surface is tropical (Figure 1a, Table 2, Online Supplemental File 1).

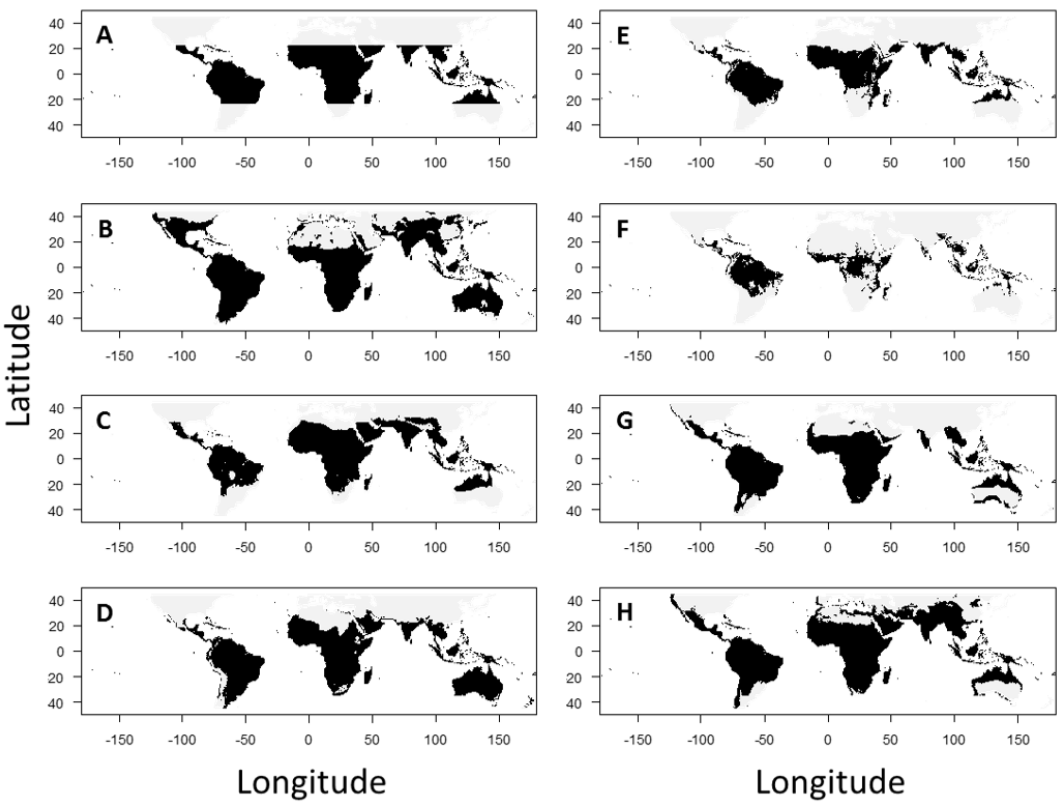

Figure 1. Maps of Earth's tropical land areas. Maps of the terrestrial tropics (black) as defined under various criteria: (a) Criterion 1 = all areas between 23.4°S and 23.4°N; (b) Criterion 2 = all areas with a net positive energy balance; (c) Criterion 3 = all areas where mean annual temperatures does not vary with Latitude; (d) Criterion 4 = all areas where temperatures do not go below freezing in a typical year; (e) Criterion 5 = all areas where the mean monthly temperature is never less than 18°C; (f) Criterion 6 = all areas where the mean annual "biotemperature" ≥24°C; (g) Criterion 7 = all areas where the annual range of temperature is less than the average daily temperature range; (h) Criterion 8 = all areas where precipitation seasonality exceeds temperature seasonality. GeoTIFF maps are available as online supplementary files 1-8.

Criterion 2: All areas of the Earth's surface that have a net positive energy balance.

Under Criterion 2, the tropics include all areas where energy from incoming solar radiation exceeds energy losses through reflection and thermal radiation (Stephens et al. 2012, Stephens and L'Ecuyer 2015). To map the extent of areas classified as tropical under Criterion 2, we averaged the monthly measures of net radiation balance provided by the NASA Earth Observations Program (https://neo.sci.gsfc.nasa.gov) for the period of January 2007 through December 2016. The net radiation data are provided at a 15-arc-minute spatial resolution but were disaggregated and masked to a resolution of 2.5 arc minutes to be comparable with the maps created for other criteria. Under Criterion 2, the tropical belt extends to approximately 35-40°N and S latitude (with localized extensions up to nearly 44°N and 48°S), and it includes many areas that are more-typically thought of as being subtropical (Corlett 2013). Of note, however, is that some areas defined as being tropical according to Criterion 1 are not defined as tropical under Criterion 2. Specifically, areas with high albedo due to arid conditions and low vegetation cover (e.g., the Sahara) are classified as being non-tropical despite occurring at low latitudes. According to Criterion 2, 45.5% of the Earth's land surface is tropical (Figure 1b, Table 2, Online Supplemental File 2).

Criterion 3: All areas of the Earth's land surface where mean annual temperatures show little or no change with latitude

A common but inaccurate generalization of the Earth's climate is that temperatures steadily decrease as one moves from the equator to the poles (i.e., as latitude increases). In fact, while temperature does decrease with increasing latitude in temperate and boreal regions (after correcting for altitude), mean temperatures actually exhibit little or no relationship with latitude near to the equator. One potential definition of the tropics is, therefore, the region where temperature is unrelated to latitude and, hence, does not differ significantly from temperatures at the equator (Wright et al. 2009). In order to map the extent of tropical areas under Criterion 3, we first created a map of Mean Annual Temperatures (MAT) correcting for altitude (i.e., at sea level). To do this we used WorldClim data (version 1.4) of estimated MAT (Hijmans et al. 2005) and altitude (m asl, 2.5-arc-minute resolution) such that $MAT_{sea\ level}$ = estimated MAT – (Elevation × 0.006) (the approximate average moist air adiabatic lapse rate is a 6°C temperature decrease per km increase in elevation; Lalas and Finaudi 1974). We then defined the tropics as all areas that have a mean annual temperature at sea level that is not markedly different from what occurs near the equator (i.e., non-tropical areas have $MAT_{sea\ level}$ that are colder than 90% of areas within ±5° latitude of the equator). According to this method, all areas with $MAT_{sea\ level}$ of ≤26°C were classified as non-tropical and all areas with $MAT_{sea\ level}$ >26°C were classified as tropical. Under Criterion 3, 35.44% of the Earth's land surface is tropical (Figure 1c, Table 2, Online Supplemental File 3).

Criterion 4: All areas of the Earth's surface where temperatures do not go below freezing in a typical year

To map the extent of areas classified as tropical under Criterion 4, we used the Climatic Research Unit's (CRU) gridded time-series dataset of average number of frost days per year for the period of 2011-2014 (Harris et al. 2014). These data are provided at a resolution of 30 arc minutes (0.5°) but were disaggregated to a resolution of 2.5 arc minute to be comparable with the maps created under other criteria. Using these data, we classified all areas that 1) have no frost days per average year and that 2) have a "Minimum Temperature of Coldest Month" greater than zero (according to WorldClim) as being tropical. Under Criterion 4, the tropics excludes some low-latitude equatorial areas that have low temperatures. For example, many high-elevation areas are excluded. Some desert areas (e.g., the Sahara) that experience severe nighttime cooling are also excluded. Conversely, some high-latitude areas with warm to moderate year-round temperatures (e.g., coastal areas up to 60°N and S) are included as tropical. According to Criterion 4, 39.0% of the Earth's land surface is tropical (Figure 1d, Online Supplemental File 4).

Criterion 5: All areas of the Earth's surface where the mean monthly temperature is never less than 18°C

This criterion is based on the Köppen and Trewartha Climate Classification Systems (Trewartha 1943, Peel et al. 2007, Belda et al. 2014), which were originally derived on the basis of vegetation zones (Holdridge 1947, Holdridge 1967). To map the extent of land areas classified as tropical under Criterion 5, we used the Worldclim 2.5 arc minute resolution maps of mean monthly temperatures and identified areas for which the minimum Mean Monthly Temperature ≥18°C. As above, under Criterion 5 some high-elevation and desert equatorial areas are excluded from the tropics. Indeed, given the adiabatic lapse rate of approximately -6°C km^{-1} elevation, nearly all montane areas above around 1300-1500 m asl are excluded from the tropics regardless of latitude. According to this criterion, 26.5% of the Earth's land surface is tropical (Figure 1e, Table 2, Online Supplemental File 5).

Criterion 6: All areas of the Earth's surface where the mean annual biotemperature is ≥24°C

Biotemperature is the mean annual temperature with all temperatures ≥30°C or ≤0°C adjusted to zero to reflect the fact that plants are generally dormant at these extreme hot or cold temperatures. This criterion is based on the Holdridge life zone system (Holdridge 1947, Holdridge 1967). To map the extent of areas classified as tropical under Criterion 6, we used the Worldclim 2.5 arc minute resolution maps of Mean Monthly Temperatures and reclassified all temperatures

≥30 or ≤0°C as 0°C. We calculated the biotemperature for each land pixel as the mean annual temperature including adjustments. We then identified all areas for which the biotemperature is ≥24°C. Criterion 6 is highly conservative and excludes many low-latitude areas or areas that are classified as tropical under the other criteria presented above and below. For example, equatorial highland areas are excluded, as are large parts of lowland Africa (e.g., much of Cameroon and Gabon) where biotemperatures are less than 24°C. Under Criterion 6, just 15.47% of the Earth's land surface is classified as tropical (Figure 1f, Table 2, Online Supplemental File 6).

Criterion 7: All areas of the Earth's surface where the annual temperature range is less than or equal to the average daily temperature range

The ratio between seasonality and the daily temperature range (DTR) is sometimes referred to as isothermality (Chan et al. 2016). As such, according to Criterion 7, the terrestrial tropics include all parts of the Earth's land surface with isothermality <1 (Laing and Evans 2015). To map the extent of areas classified as tropical under Criterion 7, we first used the WorldClim 2.5 arc minute Mean Monthly Temperature data to determine the range of annual temperatures as the maximum monthly mean temperature – minimum monthly mean temperature (note that this approach differs slightly from the BIOCLIM method for calculating isothermality in which the annual temperature range is calculated as the hottest monthly mean maximum temperature minus the coldest monthly mean minimum temperature; under the BIOCLIM methods, it is impossible for the DTR to exceed the annual temperature range; Hijmans et al. 2005, Booth et al. 2014). We then calculated the DTR as the mean difference between monthly average maximum and minimum temperatures. All areas where DTR exceeds the range of annual temperatures were classified as tropical. According to Criterion 7, 34.5% of the Earth's land surface is tropical (Figure 1g, Table 2, Online Supplemental File 7).

Criterion 8: All areas of the Earth's surface where the seasonality in precipitation exceeds the seasonality in temperature

To map the extent of areas classified as tropical under Criterion 8, we compared the standard deviation of monthly mean temperatures provided by the WorldClim 2.5 arc minute datasets to the coefficient of variation (CV) in monthly precipitation. Areas where the standard deviation of temperatures (°C × 10) is less than the CV of monthly precipitation were classified as being tropical (Laing and Evans 2015). Since this criterion does not take into consideration absolute temperatures, and rather only the seasonality of temperatures, the tropics extend to aseasonal high-latitude areas including the western coasts of the northern USA and Canada up to over 60°N, the western coast of Chile, and the southern coast of Australia. According to Criterion 8, 44.1% of the Earth's land surface is tropical (Fig. 1H, Table 2, Online Supplemental File 8).

Other definitions

Several other definitions of the tropics have been proposed (Laing and Evans 2015), although they remain less commonly employed than the eight criteria presented above. For example, the tropics have sometimes been defined as the region extending a set number of latitudinal bands from the equator (Gelaro 1992), the region enclosing the mean Hadley circulation cells

Table 2. The extent and climate of land areas defined as being tropical under different criteria. See Table 1 for descriptions of each criterion, Figure 1 for maps of tropical land areas under each criterion, and Supplemental Online Table 1 for citations and classification of tropical studies.

Criterion	Land area (10^6 km^2)	Southern latitudinal extent (°S)	Northern latitudinal extent (°N)	Maximum altitude (m asl)	Minimum MAT (°C)	Maximum MAT (°C)	Percent of "tropical" studies (%)
C1	50.191	-23.40	23.40	5804	-4.4	31.9	84.98
C2	68.386	-47.52	44.73	7088	-17.8	31.9	97.71
C3	53.233	-30.44	34.19	7088	-13.5	31.9	72.48
C4	57.713	-48.85	39.73	4192	4.5	31.9	90.37
C5	39.839	-28.56	28.40	2133	18.2	31.9	91.28
C6	23.241	-25.44	27.73	1941	24	29.6	51.83
C7	51.851	-55.98	45.81	6269	-10.8	31.5	71.10
C8	66.207	-54.44	62.40	7088	-14.5	31.9	96.33
Any	79.628	-55.98	62.40	7088	-17.8	31.9	99.56
Most	51.555	-40.73	32.98	6269	-4.4	31.9	86.70
Most– excluding C1	53.216	-40.73	32.98	6269	-8.7	31.9	90.83
Core	21.223	-23.40	23.40	1941	24	29.6	44.04
Core – excluding C1	21.237	-24.73	24.98	1941	24	29.6	44.04

(equating to ~30°N-30°S; Bellon et al. 2011), the region where mean monthly temperature variation between the average of the three coldest and three warmest months is less than 5°C (Evans 1992), the region where average precipitation equals average evaporation (Fosberg et al. 1961), and the region where the net radiation balance equals or exceeds 80 kg-cal/cm^2 a year (Fosberg et al. 1961). Alternatively, the tropics have also been defined based on the range extent of local "tropical" taxa such as palms and mangroves (e.g., Houston et al. 1891), or coral reefs in marine systems (Spalding and Grenfell 1997).

Literature review: Are tropical studies being done in the tropics?

To examine the modern usage of "tropical" in the scientific literature compared to the eight definitions of the tropics as presented above, we extracted the coordinates of study locations for studies published in 2014, 2015, and 2016 in two of the leading academic journals focused explicitly on tropical biology and conservation: *Biotropica* and *Journal of Tropical Ecology*. Articles published as part of special issues or without obvious study locations were excluded from consideration resulting in a total of 233 "tropical" study sites (103 sites from articles in *Biotropica* and 130 sites from articles in *Journal of Tropical Ecology*). We then extracted information on the climatic conditions occurring at each of these sites and their classification as tropical vs. non-tropical according to each of the criteria defined above (see Supplemental Table 1 for article citations and information).

The study sites of the "tropical" articles ranged from 32.4°S to 29.9°N latitude and from sea level to over 5000 m asl elevation, with mean annual temperatures ranging from -0.4 to 29.4°C (and total annual precipitations ranging from 140 to 7393mm yr^{-1}; Table 1). 44% of tropical studies occurred in the core tropics; 87% (91% if allowed to extend to latitudes >23.4°) occurred in areas that are tropical by most definitions, and only 1 (0.4%) study occurred in an area (Eastern China) that does not meet any of the criteria presented above (Fig. 2B). The criterion that included the greatest percentage of tropical studies was C2 (98% of all studies; "*All areas of the Earth's surface that have a net positive energy balance*.") followed by C8 (96% of all studies; "*All areas of the Earth's surface where the seasonality in precipitation exceeds the seasonality in temperature*"). The criterion that included the fewest studies was C6 ("*All areas of the Earth's surface where the mean annual 'biotemperature' is ≥24°C*") with just 52% of studies.

Discussion and conclusions

While all eight main definitions of the tropics differ in geographic location and extent, they share a common core area (Figure 2A). More specifically, all definitions include most low-elevation equatorial regions as being tropical. This core area covers approximately 21.230 × 10^6 km^2 and represents 14.1% of the Earth's land surface. If this core area were allowed to extend beyond 23.4° North/South (i.e., disregarding Criterion 1), it would include an additional 14,000 km^2 of land area. If we are less conservative and include all areas satisfying at least a majority of the criteria (i.e., 4 or more, excluding Criterion 1), then the tropics expands to an area of 51.703 × 10^6 km^2 (34.4% of Earth's land surface). This area that is "tropical by most definitions" conforms well to the tropical latitudes defined under Criterion 1 (i.e., between 23.4° North/South) with a few notable exceptions being extensions into northern Mexico, southern Florida USA, southern Africa and South America, and south coastal Australia, along with the exclusion of the extreme arid areas of the Sahara and the Arabian Peninsula. Over half of the Earth's land surface (51.9%; 77.887 × 10^6 km^2) can be considered

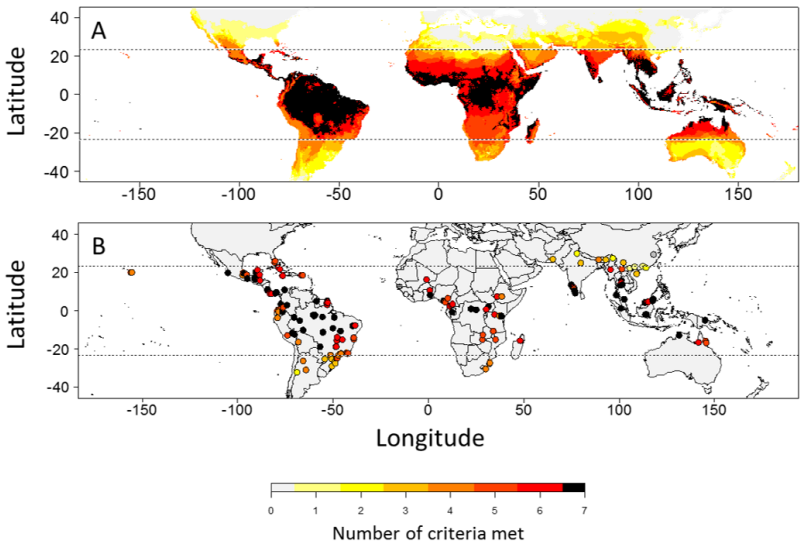

Figure 2. Where are the tropics and where are tropical studies being conducted? (a) The number of climatic criteria (Criteria 2-8) satisfied (23.4°S and 23.4°N as defining Criterion 1 are shown as horizontal dashed lines). The core tropics where all criteria are met are colored black. (b) The location of recent "tropical studies" published in *Biotropica* and the *Journal of Tropical Ecology* (See Supplemental Table 1 for article citations and information). The color of points indicates the number of climatic criteria (criteria 2-8) satisfied (23.4°S and 23.4°N as defining Criterion 1 are shown as horizontal dashed lines).

tropical under at least one of the eight criteria described above (Fig. 2A). It should be noted that our maps of the tropics, and hence the quantifications of tropical land area, are to some degree arbitrary as the exact limits delineating tropical vs. non-tropical areas under any definition will depend on many different factors including the specific formulation of the criterion and climatic variables, as well the accuracy and resolution (temporal and spatial) of the underlying data. Beyond the limits, the distinctions between tropical vs. non-tropical areas are more marked and thus less ambiguous.

The tropics can be delineated from the non-tropics in many different ways. Maps of the terrestrial tropics based on different aspects of climate or energy flux share a great deal of overlap but can also differ in some significant and important aspects (Fig. 1, Table 2). Applying different definitions of the tropics will influence our understanding of the roles that tropical systems and species play in ecology and evolution as well as the responses of the tropics to climate change. For example, under Criterion 1, the extent of the tropics is based strictly on the angle of the Earth's inclination and, thus, will not be affected by any anthropogenic activities - including climate change (but see Adhikari and Ivins 2016). Indeed, because of changes in the Earth's tilt, the tropics as defined under Criterion 1 are contracting by approximately 0.5 arc seconds (~15 meters) per year (Berger 1976). In contrast, under all other criteria, the changes in energy flux and climate that are occurring due to the greenhouse effect and anthropogenic climate change are causing a widening of the tropical belt (and encroachment into higher elevations; Fu et al. 2006, Lu et al. 2009, Quan et al. 2014). It has been argued that the global tropics have already expanded by approximately 1-3° latitude in each hemisphere since 1979 because of climate change, with an average expansion rate of 0.5-1.0° latitude per decade (Lucas et al. 2014). Likewise, a growing number of studies show that some tropical species are already migrating to higher latitudes and/or elevations to track suitable climates, leading to consequent effects on biodiversity and ecosystem function (e.g., Colwell et al. 2008, Feeley et al. 2011, Freeman and Freeman. 2014, Duque et al. 2015, Lenoir and Svenning 2015, Pecl et al. 2017).

The purpose of this paper is not to propose that any single definition of the tropics be used exclusively, rather our intention is to highlight how different definitions vary in what land areas are classified as tropical vs. non-tropical, as well as how the distribution of recent "tropical" studies compare to formal definitions. Given that there is no single universally accepted definition of the tropics, and that different definitions of the tropics can differ so markedly in their extent and location, we encourage future researchers to be clearer and more precise when describing their study systems and species (e.g., as a minimum, the geographic coordinates and elevations of all study sites should be included in publications). By improving our understanding of what areas are tropical or not, we can more accurately assess the degree to which different species and systems are represented in current studies and datasets; this in turn will help to direct future research and conservation efforts.

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Online Supplemental Files

Online Supplemental Table 1. Excel file (.xlsx) listing citations and information of tropical studies included in the analyses of study locations.

Online Supplemental File 1: GeoTIFF map of the tropics as defined under Criterion 1 = All areas of the Earth's surface that receive direct solar radiation at some point during the year.

Online Supplemental File 2: GeoTIFF map of the tropics as defined under Criterion 2 = All areas of the Earth's surface that have a net positive energy balance.

Online Supplemental File 3: GeoTIFF map of the tropics as defined under Criterion 3 = All areas of the Earth's land surface where mean annual temperatures show little or no change with latitude.

Online Supplemental File 4: GeoTIFF map of the tropics as defined under Criterion 4 = All areas of the Earth's surface where temperatures do not go below freezing in a typical year.

Online Supplemental File 5: GeoTIFF map of the tropics as defined under Criterion 5 = All areas of the Earth's surface where the mean monthly temperature is never less than 18°C.

Online Supplemental File 6: GeoTIFF map of the tropics as defined under Criterion 6 = All areas of the Earth's surface where the mean annual biotemperature is ≥24°C.

Online Supplemental File 7: GeoTIFF map of the tropics as defined under Criterion 7 = All areas of the Earth's surface where the annual range of temperature (seasonality) is less than or equal to the average daily temperature range (DTR).

Online Supplemental File 8: GeoTIFF map of the tropics as defined under Criterion 8 = All areas of the Earth's surface where the seasonality in precipitation exceeds the seasonality in temperature.

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