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Evaluating General Vegetation Models using Floristic Data

Abstract

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This volume invites papers that connect floras, i.e. species, with concepts of vegetation, which may or may not be based directly on species. There is a long history of attempts to relate vegetation to climatic conditions, but only a very few attempts to relate species to climate. This study demonstrates how widely available floristic data can be used to evaluate non-floristic models that describe vegetation by means of its structure and constituent plant types, using the climatic limits of those types. Climatic envelopes have been criticized strongly as based only on “empirical” relationships, and the accuracy of the first world climatic-envelope model, for 90 plant types, was only “fair”. That first envelope model, however, was improved by adding better estimates of potential evapotranspiration and critical minimum temperatures, better representation of foliage types; and by increasing to 115 the number of plant types. That model, now much more accurate, still lacks a formal, global validation. This short paper demonstrates how such a worldwide validation might be done, where the necessary floristic and pheno-morphological data are available.

Key words: basic ecological plant types, climatic envelope models, field-site climates, model validation, PFORMS model.

Introduction

Few researchers have made such major contributions as has our honoree Sandro Pignatti to the study of *both* floristics (*Flora d'Italia*, Pignatti 1982) and vegetation (*I Boschi d'Italia*, Pignatti 1998). So it is especially fitting that the theme of this volume invite papers that connect floras (i.e. plant species) with vegetation types, which are often described non-floristically. Relatively few treatments have attempted to compare floristic vs structural classifications of vegetation (e.g. Werger & Sprangers 1982). This study demonstrates how widely available floristic data can be used to evaluate non-floristic models that describe vegetation by means of its structure and constituent plant types, using the climatic limits of those plant types.

A system for identifying and naming plant species has existed since the time of Linnaeus, and most parts of the world have inventoried their plant species to some extent. From these data, systems of floristic units have been derived by the rules of phytosociol-

ogy (Braun-Blanquet 1964; Mueller-Dombois & Ellenberg 1974) and arranged hierarchically and named according to the rules of phytosociological nomenclature (Theurillat & al. 2020). Records of species occurrence, in the form of Braun-Blanquet relevés or other common formats, are available for many thousands of sites worldwide, as collected in the GIVD (Dengler & al. 2011) and other data bases. Floristic richness has been mapped at global scale by Barthlott & al. (1996). Floras and species, however, are regional if not local, and only a handful of the world's species extend their ranges to different continents or other large regions, especially across the Equator.

Vegetation, on the other hand, may be described by floristic units or by pheno-physiognomy, dominance types, strata, synusiae, or by main constituent plant types (Poore 1962; Whittaker 1973; Beard 1978; Barkman 1979; Werger 1988). Plant types defined entirely by structure, such as deciduous broad-leaved trees, stem-succulents or graminoids, had been called “growth forms” (*Wuchsformen*) by Drude, based on the *Hauptformen* of Humboldt (1806), the 54 types of Grisebach (1872), and his own 55 postulated forms (Drude 1896; Barkman 1988). Structural types interpreted as ecologically significant adaptations to environmental conditions were called ‘life forms’ (*Lebensformen*) by Warming (1895) and could be interpreted as basic ecological types, grouping taxa with similar form and ecological requirements, resulting from similar morphological responses to similar environmental conditions. A very comprehensive, global classification of plant life forms is found as Appendix A in Mueller-Dombois and Ellenberg (1974). Attempts to relate plants and plant types quantitatively to climatic conditions began in the late 1800s, focusing especially on temperature limitations. Studies in northern Europe, for example, suggested that temperate-zone deciduous trees require four months of mean temperature above 10°C in order to reproduce (Enquist 1924, 1929, 1933; Rubinstein 1924).

Vegetation types have been recognized, mapped and related, however qualitatively, to climatic conditions since the mid-1800s (e.g. Grisebach 1838, 1866, 1872; Schimper 1898; see de Laubenfels 1975). Systems of vegetation types are usually defined fairly generally, especially over large areas, and may be at least as numerous as there are or have been different researchers. The best world maps of “natural” vegetation (Schmithüsen 1976) are based on a legend with about 175 types, most defined without reference to floristics. There are many other noteworthy world-scale vegetation classifications (e.g. Rübél 1930; Schmithüsen 1968; Mueller-Dombois & Ellenberg 1974: Appendix B) or other treatments (e.g. Eyre 1968; Walter 1968, 1973; Archibold 1995).

Models of vegetation over large areas are also necessarily quite general, due to the overwhelming number of individual local species and the often subjective nature of vegetation descriptions and classifications. Some, usually smaller sets of vegetation types can be predicted over large regions with some degree of accuracy from climatic relationships (e.g. Box 1978; Emanuel & al. 1985; Prentice & al. 1992; Box 1995c) and with less accuracy from satellite data (e.g. Poulter & al. 2011; Strahler & al. 1999; Tateishi & Kajiwara 1991). But it is inherently difficult to use species to evaluate vegetation models, due to the differences in concept and classificatory rigor. This obstacle can be overcome by use of an intermediary, namely the basic ecological plant types that compose the vegetation, have functional roles in vegetation (cf Gillison 1981, 2013; Chapin 1993), and can be matched with actual species. Basic ecological types, such as summergreen broad-leaved

trees or tall grasses, are generally described by pheno-physiognomy, i.e. combinations of plant architecture and seasonal foliation or other activity pattern. Over broader areas, the occurrence of such basic plant types can also be related to climatic factors (Box 1981a). Despite the long history of attempts to relate vegetation types to climate, there have been relatively few attempts to relate species to climate (e.g. Box & al. 1993; Iverson & al. 1999).

The purpose of this paper is to demonstrate how available floristic data can be used, even over very large areas, to evaluate predictive, non-floristic models of vegetation based on concepts of basic ecological plant types. As a demonstration, this is done herein only at a few geographically scattered sites, where the necessary data were available to the author. The procedure is simple: sites were selected within the world’s main bioclimatic macro-regions (see Table 1; Walter 1970) based on data availability and balanced geographic representation of the world’s main climatic regions. Then, local species are matched to the different plant forms predicted by the model, and results are shown for five sites ranging from Northern high latitude to tropical mountains to southern Hemisphere woodland.

Table 1. Minimum Location Needs for Evaluating World Vegetation Models.

This list totals 15 major climatic situations that should be represented in even the most minimal attempts to evaluate global vegetation models. The Roman numerals indicate corresponding Walter climate types (Walter 1970). A more detailed list of world bioclimatic types and regions, based on Walter, was given in Box (2016).

Tropical [wooded]:	Humid (equatorial: I)	Evergreen [rain]forest
	Wet-dry (II)	Raingreen forest/woods
	Dry (Ia, I-III)	Scrub (usually semi-evergreen)
Mountains (esp II):	montane belt	Evergreen/semi-evergreen forest (I,II)
	alpine belt	Páramo (I) or puna (II)
Temperate humid	Warm-temp. (Ve)	Laurel or other evergreen BL forests
	Cool-humid (V,Vm)	Laurel or other evergreen BL, conifer or mixed forests
	Cold-winter (VI)	Summergreen forest
Mediterranean	Mediterranean (IV)	Sclerophyll woods/shrublands, dwarf scrub (usually mixed)
Subhumid	Tropical (II-III)	Savanna (trees deciduous, evergreen or mixed)
	Temp. Continental (VII)	Temperate grasslands (caducous except highly maritime)
Semi-Desert	Subtrop. Arid (III)	Taller semi-desert, with many evergreens (e.g. succulents)
	Temp. Arid (VIIa)	Shorter, shrubby semi-desert, mostly caducous
Boreal (humid)	Boreal (VIII)	Conifer or BL forest/woods (evergreen, deciduous, mixed)
Polar	Polar (IX)	Tundra (herbs + dwarf shrubs, some evergreen under snow)

Background

In order to explore the advantages and environmental relationships of particular plant forms and adaptations, plant types must be described by identifiable form characters with hypothesized functional significance. Literature (e.g. Schimper 1898; Rubel 1930; Schmithusen 1968; Walter 1968, 1973) and experience both suggest that the most important form characters should involve aspects of the:

- permanence of above-ground, light-capturing plant structure (e.g. woody versus non-woody);
- overall size of plants, especially relative to other plants;
- architecture of plant structure, including attributes of leaves or other photosynthetic surfaces; and
- seasonal activity of the plants, which may be much more complex than just ever-greenness or deciduousness.

These characters are paramount since plant metabolism, transpiration and other processes operate largely through the size, green surface area, and surface consistency of plants, and their seasonal variations. The apparent main characters needed for identifying basic plant types have been summarized, *inter alia*, by Box (1995a) and incorporated in the original concept of "plant functional types" (e.g. Smith & al. 1993; Box 1996).

The distributions of particular plant species and more general ecological types are determined by adaptations to environmental factors, especially climate. As a result, basic plant types should be described largely by pheno-morphology (or pheno-physiognomy), involving the characters identified above. Relationships between plant form, climate, and plant function have been summarized by many authors (and contradicted by others). The first systematic attempt to relate general vegetation types to climate, at global scale, was probably that of Rubel (1930), which postulated upper and lower limits relative to the most commonly available measures of temperature and water availability; a more unified but otherwise similar approach was the life zones of Holdridge (1947). This limitation approach was eventually applied by means of hypothesized climatic envelopes to vegetation types (Box 1978) and then expanded to predict the worldwide occurrence of structurally defined plant growth forms (Box 1981a). This initial growth-form model involved:

- 1) a set of 90 plant forms, each defined by pheno-morphologic characters and together representing the main growth forms in world vegetation;
- 2) a model of the effective climate, using eight variables for which data can be obtained or estimated reliably worldwide; and
- 3) a climatic envelope for each plant type, for predicting where it could occur, based on climatic limits.

The types for the world model were generated by a sort of "geographic regression" that postulated the growth forms needed to represent world vegetation and then filled in the gaps iteratively. The procedure started with basic structural types (trees, shrubs, graminoids, etc.) and added leaf types, seasonality patterns and leaf consistencies in known species, with examples of each type postulated (see Appendix A in Box 1981a). Each plant form is defined by six form characters, which means that this information must be available for species in order to match them with their corresponding form (or forms). For each plant type, a hypothesized climatic envelope was constructed, based on apparent

theoretical and empirical climatic limits to the geographic ranges of prototype species. This combined model of plant types, effective climate, and climatic limits was then used to predict the possible occurrence of the plant types at climatic sites worldwide (Box 1981a). The original purpose of that model was to demonstrate the great degree to which the geographic occurrences of basic ecological plant types (as defined above) are delimited by climatic conditions. Beyond that, though, the model also proved to be a useful means of clarifying climatic (and other environmental) limits and limiting factors, and for testing related hypotheses.

Ever since their introduction, climatic envelopes have been criticized strongly as being “empirical” and not sufficiently theoretical for coupling with the global climate models (GCMs) being developed (cf Levis & al. 2000). The criticism was largely justified, and the predictive accuracy of that first world climatic-envelope model for plant types was rightly judged as only “fair” by Mucina (2018). That first envelope model, however, was improved greatly by adding:

- 1) a more globally reliable estimate of potential evapotranspiration (Box 1986, 1987);
- 2) absolute minimum temperature as an envelope variable (Box 1995b, c; cf Sakai 1971); and
- 3) shade-tolerant laurophylls as a basic leaf type (Box 1997; cf Box & Fujiwara 2005, 2013).

Accuracy was also improved through re-calibration of limiting values based on field checks, however brief, in about 50 countries on all continents except Antarctica. As a result, the model is now fairly accurate, although it still lacks a new, global validation.

Each envelope (plant form) is a separate model, which was calibrated by another sort of “regression”, which predicts plant-form spectra at sites and checks them against known occurrences of taxa that correspond to the particular plant forms. Calibration involved adjusting envelope limits, iteratively and worldwide, to include known occurrences and exclude errors. The whole set of plant forms was also made more geographically balanced by including more understorey forms in all regions. The combined model, now known as PFORMS, is constantly being modified and now includes about 115 plant forms (see list in Box & Fujiwara 2005), defined by basic structural type, relative plant size, type of leaf or other photosynthetic organ, relative leaf size, seasonality habit, and consistency of the photosynthetic surface (see table in Box 2019). This model is fairly well known, having been cited in works on plant functional types (e.g. Smith & al. 1997), world vegetation modeling (e.g. Peng 2000; Poulter & al. 2011), and shortcomings of ecological research in general (e.g. Peters 1991; Mucina 2018). The idea (Box 1984) to use basic ecological plant types in a first dynamic model of the growth and structural development of vegetation stands worldwide (cf Box 1980, 1981b) could not be pursued at the time, but this idea was adopted by subsequent global modeling efforts (Cramer & Leemans 1993; Foley 1995; Cramer 1997).

Model accuracy has not been formally quantified, since evaluation of this and other large-area models would require decades of travel, money, field experience, and data from most parts of the world. Since this is obviously not possible in the short term, the purpose of this paper is only to give some examples.

Methodology and Data

The methodology requires sites with relevés or other adequate field data and good familiarity (to the author) with local species and their pheno-morphological attributes, which permits assigning species to particular plant forms. The procedure involved the following steps:

- Construction of a world data file for climatic conditions at available field sites;
- Prediction by model PFORMS of the plant forms possible climatically at these sites;
- Identification of actual local species that correspond to the plant forms predicted;
- Identification also of species that occur but do not correspond to any plant form predicted;
- Selection of a small but geographically representative sample of these results to present herein.

This is not an attempted model validation, only a demonstration of how such model evaluations could be done with available data. The most minimal model evaluation would require well-chosen locations in at least 15 of the world's main climatic regions (Table 1; see Conclusion section).

Since climatic models automatically imply areas of some size around climate sites (or across pixels), all kinds of species occurrence data are valid, provided only that the species occur on sites that are not unusual topographically, edaphically or otherwise (e.g. wetlands). Species occurrence can thus be determined from any combination of relevés, local species lists (as from protected areas), species range maps, and targeted field observations. Assigning species to plant types, however, requires reliable knowledge of the main phenomorphological characters of the species. This must be based on field observation by the author (with local botanists) but may also involve photos and verbal descriptions (as on the Internet) and the rare literature treatments that do describe the pheno-morphological characteristics of the species. Nevertheless, the relevés made by the author and colleagues, following the Braun-Blanquet methodology (Fujiwara 1987), plus field notes on form characters, do provide some data from many world regions and most major climatic situations (cf Table 1). These records are from 37 countries or other large regions, often with multiple local areas, and include the roughly 1400 relevés from the Eastern North American Vegetation Survey (1988-90; see Miyawaki & al. 1994); extensive fieldwork across much of East Asia (cf Fujiwara 2008; Fujiwara & Harada 2015); fieldwork in all five of the world's regions of Mediterranean-type climate; and fieldwork in tropical and subtropical areas including Kenya, Brazil, the tropical and subtropical Andes, Mexico, Kerala, Myanmar, northern Borneo, and Australia. Field data are also available from much of Europe, Georgia (Caucasus), Argentina and New Zealand, as well as the USA and Canada.

Candidate field sites for the examples herein were selected, with increased density in areas of greater topographic or climatic complexity, and numbered about 300. Each site had to have species lists and other descriptions available (on line or in printed literature), and had to have been visited and described by the author (with local colleagues) with at least one formal relevé. Climatic data were then gathered (from the author's data-base) from stations at or near these field sites. All climate data are from before 1980, in order to minimize effects of differential global warming. Since most field sites were not at meteorological stations, their climatic profiles had to be estimated by triangulation from nearby sites coupled with projection of mostly lowland data to the elevations of the field invento-

ries. This was done by program POLATE, described briefly in Box (2019), using a value of 5.6°C/1000m for the terrestrial lapse rate over terrain (as opposed to 6.4°C/km in the free atmosphere).

Absolute minimum temperature is a much-overlooked factor (Sakai & Larcher 1987) and is not recorded everywhere (and often for only a few years even where it is recorded). It is also not “strongly correlated” with mean temperature minima (as stated erroneously by Woodward & al. 2004) but rather has a geography of its own (Box 1995b). Absolute minimum temperature is thus estimated for all sites herein based on the difference between mean monthly minimum and absolute minimum at nearby sites where this difference is known (model TXTRAP); then the lower of the measured or estimated values is used. This procedure recognizes, for example, the much greater difference between mean minima and absolute minima in eastern North America than in East Asia at the same latitudes (see Box 1995b). The climatic moisture balance is defined as annual precipitation divided by annual potential evapotranspiration.

Prediction of plant forms at sites is done by applying the PFORMS model to the climatic data for the field sites, with results expressed as stand profiles organized by synusiae. Results consist of predicted plant-form profiles with corresponding, actually occurring corresponding species juxtaposed. Examples are shown in the next section. About 20 sites had relatively complete results, but this short paper shows detailed results for only five widely separated sites, selected to represent quite different climates on four continents and based mainly on ability to get the necessary information on species occurrence and characters quickly, while retaining geographic scattering. The first three sites selected are near meteorological stations, but the other two rely on estimation of site climatic conditions from nearby data.

The first site selected was Palermo (coastal northwestern Sicily), since its form-species matching had already been done (Box 2019). The natural vegetation around Palermo is open, semi-evergreen Mediterranean scrub with a diverse mix of sclerophyllous, deciduous and caducous forms (Guarino & Pasta 2017). Matches of plant taxa to particular plant forms were based on field notes from four visits to Palermo, supplemented by images and verbal descriptions from numerous websites, including Wikipedia. Species names and verification of native or naturalized status were based largely on the checklist of the Sicilian flora by Raimondo & al. (2010), greatly assisted by Riccardo Guarino. Palermo is representative of model results and potential accuracy at most sites studied. It is used here as an example because: 1) its species had already been determined from an earlier study; and 2) it is representative for open vegetation in a Mediterranean-type climate. It also illustrates the premise that warm, subhumid climates, such as the Mediterranean type in southern Italy, have unusually high richness in co-existing plant types (Box 2019).

Athens, in the upper piedmont of northern Georgia (southeastern USA), was selected because its species-form matchings could be done quickly (the author’s home) and because it is a typical example for [warmer] temperate deciduous forest in the Northern Hemisphere. The natural vegetation is summergreen deciduous *Quercus-Carya* forest, with *Acer*, *Fraxinus*, *Liriodendron* and *Nyssa* (all deciduous) plus mainly summergreen understorey trees (e.g. *Cornus florida*, *Prunus serotina*), shrubs and forbs. Matches of plant taxa to particular plant forms were determined from experience with the local species, local fieldwork, and from range maps in Radford & al. (1968, for the nearby

Carolinas). Species names are from Radford & al. (1968) and Jones & Coile (1988); lichen names are from CRMS (2011) and CNALH (no date).

The other three sites were selected for geographic diversity but had to include some representation of tropical and high-latitude vegetation. For high latitude, Tromsø (near-coastal northern Norway) was selected because: 1) it is representative of interesting high-latitude maritime situations (as also in Beringia and even Tierra del Fuego); and 2) it has a manageable number of species that could be understood quickly. Its natural vegetation is low birch woods (Dierßen 1996), as found also in some other maritime boreal areas (Walter 1974; Krestov 2003). Matches of plant taxa to particular plant forms were determined from two short field visits, from descriptions in Lid (1985) and Nilsson (1991), and from images on the Internet. Species names are as used at the time and place; lichen names are from Frisch & al. (2020).

For the tropics two sites were selected, one in equatorial high mountains and the other in a tropical wet-dry lowland. The mountain site is in the inner-tropical but seasonal alpine belt at Piedras Blancas (4150 m), in the Venezuelan Andes above Mérida. The actual vegetation, called páramo, is an open scrubland dominated by *frailejones*, i.e. *Espeletia* tuft treelets (caulirosettes) of up to 2 m. This is a relatively well studied site (e.g. Cuatrecasas 1968; Baruch 1984; Calero & Baruch 1986; Luteyn 1999; Marquez & al. 2004, 2006; Rada & al. 2019). The dominant vegetation was described by Baruch (1984) as involving three vegetation strata: an arborescent layer dominated by *Espeletia* spp. and *Hypericum*; a shrub-herb layer involving especially *Senecio*, *Castilleja*, other forbs, graminoids and seedlings; and a herb layer with acaulescent rosettes, cushions (both woody and herbaceous), mosses and lichens. This site is included here as an example because: 1) it is quite different from most other parts of the world; 2) its model results are representative of the world's few tropical alpine areas (e.g. Andine puna and alpine East Africa); and 3) its species are few enough that they could be determined quickly. Matches of plant taxa to particular plant forms were determined from information available on the Internet (especially from Luteyn, no date) and from two páramo visits, the latter with field assistance by Alejandro Velázquez. Species names are as used at the time and place; lichen names are from Pérez (1987), Sipman (2002) and other references therein.

The other tropical site is Forty Mile Scrub, a semi-evergreen low-woodland site in northern Queensland, Australia. Data for its highly seasonal wet-dry climate were extrapolated (by program POLATE) from Mt. Surprise, where the annual precipitation is about 800mm and absolute minimum temperature was estimated as 1.6°C by TXTRAP. Based on those data and its somewhat higher elevation, the [infrequent] absolute minimum temperature at Forty Mile Scrub was estimated as slightly below freezing: -0.2°C. The actual vegetation is a variably open, semi-evergreen woodland dominated by a mix of raingreen and sclerophyll trees and arborescents; it was called “dry rainforest” by Fensham (1996). The site was visited and described in 1990 along with Andy Gillison, who provided many of the species identifications and much ecological insight. It has since become a national park and is relatively well studied (e.g. Westoby 1988; Bowman and Prior 2005, Dept Env. Sci. [no date], Prior & al. 2003, 2004). This site is included because: 1) it represents the tropics and the Southern Hemisphere, at least somewhat; 2) it is quite different from other tropical wet-dry areas, and as such is both interesting and a challenge; and 3) its species could be determined and matched to predicted plant forms more quickly than could other tropical

candidate sites. Matches of plant taxa to particular plant forms were determined (assisted greatly by Andy Gillison) from field notes, information available on the Internet (e.g. Dept. Env't. Sci., no date), and from Fensham (1996), Prior & al. (2003, 2004), and Williams & al. (1997) (cf Beadle 1981). Lichen names were from Archer & Elix (2017) and Sipman (2018).

This set of examples thus has some degree of global-scale representation among its five sites. The site climates were estimated as described above, by triangulation (POLATE) for the páramo and Queensland sites. Although climatic measurements may actually be available for some sites, they would be short-term and probably for later years with less stable climatic conditions. Matches of plant taxa to particular plant forms are based on the six plant characters that define the particular forms. This is necessarily an expert system, since only the author of a global system may be able to match plant forms to species consistently. Evaluation looks at the number of plant forms predicted correctly, the number predicted wrongly (i.e. not occurring), and the number occurring but not predicted.

Results

The first example is for the mediterranean climate of Palermo, in northwestern Sicily (Table 2), where the natural vegetation is a form-diverse, open, semi-evergreen scrub. With predicted woody cover of 62% maximum, the predicted result could be interpreted as open vegetation dominated by Mediterranean-type shrubs and dwarf shrubs (sclerophyll and summergreen), with scattered smaller trees and arborescents – plus exotics such as *Eucalyptus* and cacti (*Opuntia* sp. pl.). Native or naturalized species examples are apparent for most predicted plant forms, but some species that do occur are not represented by predicted plant forms. Plant forms most likely to be predicted but not occurring locally are forms with inherently fewer species, including arborescents, leafless stemgreen forms, tuft forms (e.g. palms, *Yucca*), leaf- and stem-succulents, vines, ferns and epiphytes. Unpredicted but occurring widely (mainly on special microsites) are pines (*Pinus*) plus species that are hard to classify, such as the tall, tussocky cane grass *Ampelodesmus mauritanicus* and the forb *Eryngium campestre*, which though sclerophyllous could also be considered raingreen, since it does generally dry out rather completely in late summer.

Predicted plant forms and corresponding species are shown in Table 3 for Athens (Georgia, USA), where the potential natural vegetation is summergreen deciduous oak-hickory (*Quercus-Carya*) forest. Several evergreen plant forms are predicted to be at or near their northern range boundaries here, limited by extreme winter cold. Athens is beyond the natural range of lauro-sclerophyll *Magnolia grandiflora* and quasi-sclerophyll *Quercus virginiana*, but these evergreen trees do survive where planted (e.g. on campus or near old houses); *Magnolia grandiflora* also survives as escapes into nearby woods. With predicted woody cover of 75% maximum, the predicted result would be interpreted as summergreen forest, dominated (plus signs) by tree species from common summergreen tree genera such as *Quercus*, *Acer*, *Fraxinus* and *Carya*, along with typical, mainly summergreen understory shrubs, forbs, etc. Among the lichens, *Xanthoparmelia* occurs on rocks, *Cladina* on soil, *Rimelia* on trees or rocks, and *Canoparmelia* on pines (CRMS 2011).

For Tromsø (near-coastal northern Norway), predicted plant forms and corresponding

Table 2. Predicted PFORMS Model Results for Palermo.

Palermo is in coastal northwestern Sicily, where the climate is Mediterranean and the natural vegetation is a form-diverse open scrub involving both evergreen (mostly sclerophyllous) and caducous forms. Mean temperature (T) and average precipitation (P) for each month are shown across the top, followed by the annual values. The climatic variables in the PFORMS envelope model include monthly extreme values of temperature (Tmax, Tmin) and precipitation (Pmin, Pmax) plus annual biotemperature (BT), the absolute minimum temperature (Tabmin, i.e. the lowest ever measured, in this case over 51 years), and an annual moisture index (MIy, = P/PET, where PETy is the estimated annual potential evapotranspiration) (see main text, as well as Box 1981a, 1987, 2019).

The plant forms (EG = evergreen) predicted for Palermo are listed by their structural type: T = trees, ST = small trees, A = arborescents, S = shrubs, DS = dwarf shrubs (including cushions and semi-shrubs), RS = rosette-shrubs, SS = stem-succulents, G = graminoids, F = forbs, Fn = ferns, V = vines, E = epiphytes, Th = thallophytes (i.e. cryptogams). The closest limiting factor in the envelope design is shown in the third column (e.g. MIy, for moisture index), followed by the relative proximity of the form to that closest envelope limit (0-1 scale, u = upper value limiting).

The right-most column shows plant taxa at Palermo that correspond to the predicted plant forms. Non-native but perhaps well naturalized taxa are shown in parentheses; probably not naturalized but widely planted ornamental taxa (including some taxa from the famous local botanical garden) are shown in brackets. Question marks indicate missing information or, for particular taxa, unknown occurrence or naturalization status. With predicted woody cover of 62% maximum, this result could be interpreted as open vegetation dominated (model-generated plus signs) by Mediterranean-type shrubs and dwarf shrubs (sclerophyll and summergreen), with scattered smaller trees and arborescents – plus exotics such as *Eucalyptus* and cacti (*Opuntia* spp.). Unpredicted but occurring widely (mainly on special microsites) are *Pinus* spp., plus species that are hard to classify, such as the tall, tussocky cane grass *Ampelodesmos mauritanicus* and the forb *Eryngium campestre*.

Matches of plant taxa to particular plant forms were based on field notes from four visits to Palermo, supplemented by images and verbal descriptions from numerous websites, including Wikipedia. Species names and verification of native or naturalized status were based largely on the checklist of the Sicilian flora by Raimondo & al. (2010), greatly assisted by Riccardo Guarino.

Palermo (Sicily) 38.12°N, 13.35°E, 71m														
T	10.2	10.8	12.8	15.1	18.3	22.2	24.8	25.1	23.1	19.1	15.3	11.9	17.4°C	Tabmin = -1.7 (51 years)
P	71	43	50	49	19	9	2	18	41	77	71	62	512 mm	
BT = 17.39, MIy (P/PET) = 0.55, PETy = 926 mm														
T	Mediterr. Sclerophyll Trees							MIy	.05	<i>Quercus ilex</i> , <i>Ceratonia siliqua</i> , <i>Olea europaea</i>				
	Tall Sclerophyll Trees							MIy	.05	<i>(Eucalyptus camaldulensis Euc. globulus)</i>				
	Xeric Raingreen Trees							Tmin	.01	<i>(Jacaranda ovalifolia; Acacia spp.?)</i>				
ST	+ Dwarf-Needle Small Trees							MIy	.15	<i>Juniperus phoenicia</i> , <i>J. oxycedrus</i> ; <i>Erica arborea</i> (<i>Cupressus semperv.</i>)				
	Raingreen Small Trees							Tmin	.11	<i>(Albizia julibrissin, Acacia karroo, Erythrina viarum?)</i>				
A	Xeric Stemgreen Arborescents							MIy	.23	<i>Calycotome spinosa</i> , <i>Cytisus scoparius</i> , <i>Spartium junceum</i> , <i>Genista</i>				
	Raingreen Arborescents							Tmin	.11	<i>(Euphorbia dendroides)</i>				
	Xeric EG Tuft-Arborescents							Tmin	.11	<i>Dracaena draco</i> (<i>Yucca rostrata</i>)				
	Sclerophyll Arborescents							Tmin	.11	???				
S	+ Mediterranean EG Shrubs							MIy	.09u	<i>Rosmarinus</i> , <i>Phyllirea</i> , <i>Cistus</i> , <i>Halimium</i> , <i>Rhamnus alaternus</i> , <i>Lavandula</i>				
	+ Nanophyll Evergreen Shrubs							MIy	.14u	<i>Asparagus acutifolius</i> ; <i>Erica multiflora</i>				
	+ Xeric Summergreen Shrubs							Tmin	.10u	<i>Pistacia terebinthus</i> , <i>Vitex agnus-castus</i>				
	Hot-Desert Evergreen Shrubs							MIy	.18	<i>Atriplex halimus</i> , <i>Salsola oppositifolia</i>				
DS	Mediterranean Dwarf-Shrubs							Tmin	.25u	<i>Thymus</i> , <i>Thymelea hirsuta</i> , <i>Micromeria graeca</i>				
	Xeric Dwarf Shrubs							MIy	.23u	<i>Ephedra</i> spp.				
	Xeric Cushion Shrubs							MIy	.32	<i>Sarcopoterium spinosum</i> ; <i>Capparis spinosa</i> , <i>C. orientalis</i>				
	Xeric Semi-Shrubs							MIy	.32u	<i>Salvia officinalis</i> , <i>S. fruticosa</i> ; <i>Helichrysum italicum</i> , <i>Euphorbia bivanoe</i>				
RS	Xeric Rosette-Shrubs							Tmin	.36	<i>Chamaerops humilis</i> (<i>Agave americana</i> , <i>Alôë vera</i>)				
SS	Tall-Columnar Stem-Succulents							Tmin	.06	(none)				
	Arborescent Stem-Succulents							Tabmin	.42	<i>(Opuntia tomentosa, O. ficus-indica, with trunks)</i>				
	Fruitescent Stem-Succulents							MIy	.46	<i>(Opuntia robusta, trunkless O. ficus-indica)</i>				
	Compact Stem-Succulents							MIy	.04	<i>[Feroscactus, Echinocactus]</i>				
	Cryptic Stem-Succulents							MIy	.41u	<i>Sedum dasyphyllum</i>				
G	Short Bunch Grasses							MIy	.33	<i>Brachypodium phoenicoides</i> , <i>B. ramosum</i> ; <i>Stipa barbata</i> , <i>S. sicula</i>				
	Desert Grasses							MIy	.14	<i>Festuca caerulea</i> (<i>Aristida adscensionis</i> ssp. <i>coer.</i> , <i>Cenchrus ciliaris</i>)				
	Sclerophyllous Grasses							Tmin	.01	<i>Lygeum spartum</i> (<i>Stipa tenacissima?</i>)				
F	Xeric Cushion Forbs							MIy	.33u	<i>Sedum acre</i>				
	Succulent Forbs							Tabmin	.17	<i>Sedum stellatum</i> , <i>Portulaca sicula</i> (<i>Pilea microphylla</i> , <i>Kalanchoë daigr.</i>)				
	Raingreen Forbs							Tmin	.16	<i>Ferula</i> , <i>Foeniculum</i> , <i>Thapsia</i> , thistles; <i>Asphodelus</i> (geophyte)				
	Summergreen Forbs							Tabmin	.12	<i>Urtica pilulifera</i> , <i>Acanthus mollis</i> (semi-evergreen)				
Fn	Raingreen Ferns							Tabmin	.26	<i>Selaginella denticulata</i> ; <i>Cheilanthes</i> , <i>Ceterach</i> (poikilohydrous)				
V	Raingreen Vines							Tmin	.01u	<i>Vicia</i> spp. (<i>Fallopia?</i>); [<i>Bougainvillea?</i>]				
E	Wintergreen Bush Epiphytes							MIy	.28	<i>Viscum album</i> , <i>Loranthus europaeus</i>				
Th	Xeric Thallophytes							MIy	.50	<i>Arthonia</i> , <i>Acarospora</i> , et al.; crustose lichens				

Table 3. Predicted PFORMS Model Results for Athens (Georgia, USA)

Athens is in the upper piedmont of northeastern Georgia (southeastern USA), where the climate is typical humid-temperate and the natural vegetation is summergreen deciduous forest (see Delcourt & Delcourt 2000; cf Miyawaki & al. 1994). The table, format, methodology, and abbreviations are as explained in Table 2. At left are the plant forms predicted for Athens, listed by plant structural type. One topo-specific form (wetlands) is shown in brackets. The closest limiting factor is shown in the third column (e.g. Tabmin, for absolute minimum temperature), followed by the relative proximity of that form to its closest envelope limit (u = upper value limiting).

The right-hand column shows plant taxa occurring in the Athens area that correspond to the predicted plant forms. Non-native but perhaps well naturalized taxa are shown in parentheses; probably not naturalized but widely planted ornamental taxa are shown in brackets. With predicted woody cover of 75% maximum, this result would be interpreted as forest, dominated (plus signs) by tree species from common summergreen tree genera such as *Quercus*, *Acer*, *Fraxinus* and *Carya*, along with typical, mainly summergreen understorey shrubs, forbs, etc. Not predicted but occurring in slightly less cold urban areas are some evergreens such as *Magnolia grandiflora* and *Quercus virginiana*, which were planted or escaped.

Matches of plant taxa to particular plant forms were based on relevés and other experience with the local flora. Species names, verbal plant descriptions, and verification of native or naturalized status were from Radford & al. (1968) for the nearby Carolinas and from Jones & Coile (1988) for Georgia. Among the lichens, *Xanthoparmelia* occurs on rocks, *Cladina* on soil, *Rimelia* on trees or rocks, and *Canoparmelia* on pines. Lichen names are from CRMS (2011) and CNALH (no date).

Athens (Georgia, USA) 33.95°N, 83.32°W, 246m		[Monthly T: 1951-1990, P: 1951-1990]	
T	5.7 7.6 11.6 16.5 20.9 24.8 26.4 26.0 22.8	16.8 11.5 7.1 16.5°C, Tabmin = -20.0n (63 years)	
P	116 111 135 96 109 94 127 87 88	76 89 102 1230 mm	
BT = 16.48, MIy = 1.27, PETy = 972mm		Predicted cover: 75% (woody), 96% (herbaceous, spring maximum)	
T *	Summergreen BL Trees Heliophilic Needle Trees Temperate Needle Trees [Summergreen Feather Trees]	MIy Tmin MIy Tmin	.20 .15 .29 .11
		<i>Quercus</i> , <i>Acer</i> , <i>Carya</i> , <i>Fagus</i> , <i>Fraxinus</i> , <i>Nyssa</i> , <i>Liquidambar</i> , <i>Liriod.</i> <i>Pinus taeda</i> <i>Pinus virginiana</i> (<i>Taxodium</i> , <i>Metasequoia</i>)	
ST +	Summergreen Small Trees Temp-Evergreen Small Trees Dwarf-Needle Small Trees Short-Summer SG-BL Trees	MIy Tabmin MIy Tmin	.29 .02 .41 .01
		<i>Carpinus</i> , <i>Ostrya</i> , <i>Cornus florida</i> , <i>Cercis</i> , <i>Prunus serotina</i> , <i>Morus rubra</i> <i>Ilex opaca</i> , <i>Prunus caroliniana</i> , <i>Vaccinium arboreum</i> <i>Juniperus virginiana</i> <i>Betula nigra</i> , <i>Populus</i>	
A	Summergreen Arborescents Arborescent Bamboo	MIy Tabmin	.41 .00
		<i>Rhododendron nudiflorum</i> , <i>R. canescens</i> , <i>Asimina</i> , <i>Lindera</i> <i>Arundinaria gigantea</i>	
S	Summergreen Shrubs Laurophyll Shrubs Temperate Evergreen Shrubs Temperate EG Small Shrubs Needle-Leaved EG Shrubs	MIy Tabmin Tabmin Tabmin MIy	.29 .00 .00 .04 .34u
		<i>Vaccinium corymbosum</i> , <i>V. stamineum</i> , <i>Viburnum</i> , <i>Rhamnus</i> <i>Kalmia latifolia</i> <i>Symplocos tinctoria</i> (<i>Ligustrum sinense</i>) [<i>Rosmarinus</i> , <i>Elaeagnus pung.</i>] <i>Euonymus americanus</i> , <i>Vaccinium elliotii</i> <i>Juniperus horizontalis</i> , <i>J. communis</i>	
DS	Mesic Semi-Shrubs	MIy	.27
		<i>Potentilla canadensis</i> , <i>Duchesnia</i> , <i>Fragaria</i> , <i>Agrimonia</i> , <i>Amorpha</i>	
G	Tall Graminoids Tall Cane Graminoids Short Bunch Grasses Short Sward Grasses Short Bamboo	MIy Tabmin MIy MIy MIy	.31 .19 .50 .31 .01
		<i>Andropogon virginica</i> [<i>Arundo donax</i>] <i>Panicum commutatum</i> , <i>P. boscii</i> , <i>P. dichotomum</i> , <i>Danthonia spicata</i> <i>Uniola latifolia</i> , <i>Tridens flavus</i> [<i>Phyllostachys</i>]	
F	Summergreen Forbs Semi-Evergreen Forbs Spring-Ephemeral Geophytes Laurophyll Forbs	Tabmin Tabmin Tmin Tabmin	.44 .04 .09 .00
		<i>Polygonatum biflorum</i> , <i>Solidago arguta</i> , <i>Commelina</i> , <i>Boehmeria</i> <i>Tovara virginiana</i> , <i>Elephantopus</i> , <i>Viola</i> , <i>Taraxacum</i> , <i>Hexastylis arifolia</i> <i>Iris</i> , <i>Hymenocallis</i> , <i>Lilium</i> , <i>Narcissus</i> [<i>Muscari</i> , <i>Hyacinthus</i>] <i>Chimaphila maculata</i> , <i>Mitchella repens</i>	
Fn	Summergreen Ferns Evergreen Ferns	MIy Tabmin	.20 .00
		<i>Asplenium platyneuron</i> , <i>Botrychium dissectum</i> , <i>B. virginianum</i> <i>Polystichum acrostichoides</i>	
V	Summergreen Vines Evergreen Vines	MIy Tabmin	.20 .00
		<i>Rhus radicans</i> , <i>Parthenocissus</i> , <i>Vitis</i> , <i>Campsis</i> , <i>Anisostichus</i> , <i>Cocculus</i> <i>Gelsemium sempervirens</i> , <i>Smilax</i> spp [<i>Lonicera japonica</i>]	
E	Wintergreen Bush-Epiphytes	Tabmin	.04
		<i>Phoradendron serotinum</i>	
Th	Mat-Forming Thallophtyes Xeric Thallophtyes	MIy MIy	.31 .59
		<i>Leucobryum glaucum</i> <i>Xanthoparmelia</i> , <i>Cladina subtenuis</i> , <i>Canoparmelia</i> , <i>Rimelia</i> , <i>Usnea</i>	

species are shown in Table 4. The boreal climate there is quite maritime, and the potential natural vegetation is low *Betula* woods (Dierßen 1996), rather than the predicted conifer forest, as is also the case in Beringia (Krestov 2003), northernmost Sweden, Iceland, and some other maritime subpolar areas (cf Tierra del Fuego). With an annual moisture index (P/PET) of 2.50 this prediction would be interpreted as forest of conifers *Picea abies* (evergreen)

Table 4. Predicted PFORMS Model Results for Tromsø

Tromsø is a highly maritime site above the Arctic Circle near the Atlantic coast in northern Norway, where the natural vegetation is low birch (*Betula*) woods (Dierßen 1996, see pp 107-111; cf Walter 1973). The plant forms predicted for Tromsø by the PFORMS model are shown at left, listed by plant structural type (see Table 2 for explanation of table contents and abbreviations). The closest limiting factor in the envelope design is shown in the third column (e.g. Tmax, for warmest-month mean temperature), followed by the relative proximity to closest envelope limit (u = maximum value limiting).

The right-hand column shows plant taxa occurring in and around Tromsø that correspond to the plant forms predicted. All taxa listed appear to be native (not naturalized). Not predicted but occurring is *Calamagrostis*, a genus of taller grass common in boreal areas; predicted but not seen were spring-ephemeral geophytes.

With an annual moisture index (P/PET) of 2.50 this result would be interpreted as forest of conifers *Picea abies* (evergreen) and *Larix decidua* (deciduous), plus generally shorter but perhaps more important (plus signs) *Betula* spp., which are especially important in maritime boreal areas. In reality, conifers do occur but are less important around Tromsø; relevés from a natural area in the local botanical garden involved mainly low birch forests (*Betula*), with mainly summergreen understorey shrubs and forbs but also a few more truly boreo-polar dwarf shrubs such as *Betula nana* and *Vaccinium uliginosum* (summergreen) and *Vaccinium myrtillus* (evergreen).

Matches of plant taxa to particular plant forms were determined from two short field visits, from Lid (1985) and Nilsson (1991), plus images and verbal descriptions on the Internet, especially via Wikipedia. Species names are as used at the time and place; lichen names are from Frisch & al. (2020).

Tromsø (Norway)		69.68°N, 18.92°E, 10 m					[Monthly T: 1856-1993, P: 1951-1993]							
T	-3.3	-3.6	-2.7	0.3	4.2	8.7	11.7	10.7	7.0	2.7	-0.7	-2.5	2.7°C	Tabmin = -20.1° (38 years)
P	108	88	83	62	51	56	67	77	101	134	98	104	1030mm	
BT = 3.77, Mly = 2.50, PETy = 412mm														
T	Boreal/Montane Needle Trees	Tmax	.03	<i>Picea abies, Pinus sylvestris</i>										
	Boreal SG Needle Trees	Tmax	.03	<i>Larix decidua</i>										
ST +	Summergreen Small Trees	Tmax	.09	<i>Prunus avium</i>										
	Boreal SG-BL Trees	Tmax	.05	<i>Betula pubescens, Populus tremula, Alnus glutinosa</i>										
A +	Summergreen Arborescents	Tmax	.10	<i>Betula pubescens, Sorbus aucuparia, Salix caprea</i>										
KH	Needle-Leaved EG Krummholz	Tmin	.08	<i>Juniperus communis</i>										
	Summergreen Broadleaf Khlz./Shrubs	Tmin	.05	<i>Salix lanata</i>										
	Summergreen Needle Krummholz	Tmin	.05	<i>Larix decidua</i>										
S +	Summergreen Shrubs	Tmax	.09	<i>Salix lanata, Rubus</i> spp.										
	Temperate EG Small Shrubs	Tmin	.01	<i>Vaccinium vitis-idaea</i>										
DS	EG Tundra Dwarf Shrubs	Tmin	.20	<i>Empetrum nigrum, Vaccinium myrtillus, Dryas octopetala, Phyllodoce</i>										
	SG Tundra Dwarf Shrubs	Tmin	.17	<i>Vaccinium uliginosum, Betula nana, Salix lapponica</i>										
G	Short Bunch Grasses	Tmax	.36	<i>Deschampsia</i>										
	Short Sward Grasses	Tmax	.25	<i>Festuca ovina, Poa nemoralis</i>										
F	Summergreen Forbs	Tmax	.10	<i>Cornus suecica, Solidago virgaurea, Geranium sylvaticum, Angelica sylvestris, Filipendula ulmaria, Achillea millefolium</i>										
	SG Polar/Alpine Forbs	Tmin	.20	<i>Ranunculus acris, Bistorta vivipara, Pedicularis lapponica, Melampyrum pratense</i>										
	Spring-Ephemeral Geophytes	Tmax	.07	???										
	Semi-Evergreen Forbs	Tmin	.01	<i>Taraxacum officinale</i>										
Fn	Summergreen Ferns	Tmax	.10	<i>Athyrium filix-femina, Gymnocarpium dryopteris</i>										
Th	Mat-Forming Thallophtyes	Mly	.40	<i>Polytrichum commune, Hylocomium splendens, Hypnum, Racomitrium, Dicranum</i>										
	Xeric Thallophtyes	Mly	.10u	<i>Arthonia peltigera, A. stereocaulina, Rhymocarpus neglectus, Peltigera, Usnea, Solorina</i>										

and *Larix decidua* (deciduous), plus generally shorter but perhaps more important (plus signs) *Betula* spp. In reality, conifers do occur in northern Norway but are less important in more maritime areas where growing seasons are longer and winters less cold. Actual species occurrence was determined from relevés in a natural area of the local botanical garden, which involved mainly low birch forest (*Betula*), with mainly summergreen understorey shrubs and forbs but also a few more truly boreo-polar dwarf shrubs such as summergreen *Betula nana* and *Vaccinium uliginosum*, and evergreen *Vaccinium myrtillus*.

Predicted plant forms and corresponding species are shown in Table 5 for the páramo at Piedras Blancas (4150 m). The actual vegetation is an open scrubland dominated by caulirosettes (*Espeletia* tuft treelets) up to 2m high, small-leaved shrubs (especially *Hypericum*) and dwarf shrubs, and bunch grasses (e.g. Calero & Baruch 1986; Pfitsch 1988). This area is famous for its caulirosettes, which are analogous to those of the high mountains in eastern Africa (Hedberg 1964). These high-equatorial caulirosettes have terminal tufts of large, pubescent leaves which open in the daytime (when temperatures are above freezing) and close at night (usually with frost). Surprising here was the occurrence also, at slightly lower elevation, of not so small bushes (30 cm) of *Vaccinium* (not predicted). The distinction between bunch and tussock grasses was especially difficult, since most authors seem to consider the terms synonymous. Bunch grasses are found almost everywhere; tussock grasses, on the other hand, are larger bunches, to 2 m high, as found where the densely bunched dead stems forming the tussock provide sufficient protection against winter temperatures not far below freezing, as in cool maritime climates, tropical mountains, and some temperate wetlands (e.g. in Atlantic Europe).

The most challenging of these five examples was Forty Mile Scrub, in northern Queensland (see Table 6). The natural vegetation there is described as “dry rainforest” (i.e. dry but non-eucalypt forest), with a low overstorey (5-7 m) dominated over most of the area by *Notelaea microcarpa* (*Oleaceae*), *Alectryon connatus* (*Sapindaceae*), *Austromyrtus* sp. pl., *Geijera salicifolia* (*Rutaceae*), and *Strychnos pilosperma* (*Loganiaceae*) (Fensham 1996). All of these species are evergreen, but vegetation across northern Australia is described as also including some deciduous woody species (Williams & al. 1997; Prior & al. 2003; Bowman & Prior 2005). Our one relevé was at a site with somewhat taller but still low (18 m), open (30% overstorey, 60% sub-canopy), semi-evergreen woods that included *Geijera*, *Strychnos* and *Austromyrtus bidwellii*, plus deciduous *Pleiogynium timorense*, *Gyrocarpus americana*, and *Ailanthus* (none with cover greater than 25%). Also seen nearby was a deciduous eucalypt, probably *Eucalyptus alba*, with a green, photosynthetic layer under its white outer bark (cf Walter 1973, p. 283). With P/PET of 0.67, the prediction suggests a semi-evergreen woodland of fairly short stature. Most of the forms predicted have corresponding species that could be found or inferred from literature, but the succulent forms predicted do not occur naturally in Australia. Also, the *Xanthorrhoea* spp (“Xeric evergreen tuft arborescents”) that occur over much of Australia apparently do not occur in this area of northern Queensland, and there are no “Xeric rosette shrubs” (i.e. trunkless agavoids), although *Agave* spp. do survive well in plantings. Unpredicted forms that were observed (and their species) include: tropical non-microphyll coriaceous-leaved evergreen trees (*Ficus obliqua*), tropical evergreen lianas (*Parsonsia*), epiphytic orchids (*Dendrobium linguiforme*), tropical evergreen forbs (*Crinum*), and rolled-leaved tussock forbs (e.g. *Centrolepis*, *Lomandra*), this last of which is not represented at all as a separate form in the model system.

Table 5. Predicted PFORMS Model Results for the Páramo de Piedras Blancas.

The Páramo de Piedras Blancas is a relatively well studied, ridge-top site in the inner-tropical Andes above Mérida, Venezuela (1700 m). The actual vegetation is an open scrubland dominated by caulirosettes (*Espeletia* tuft treelets) up to 2m, small-leaved shrubs (especially *Hypericum*) and dwarf shrubs, and bunch grasses (see Calero & Baruch 1986; Pfitsch 1988 and other references in the main text). At left are the plant forms predicted for this site, listed by plant structural type (see Table 2 for key to table contents and abbreviations). The closest limiting factor in the envelope design is shown in the third column (e.g. Tmin for lowest monthly mean temperature), followed by the relative proximity to closest envelope limit (u = upper value limiting).

The right-hand column shows plant taxa occurring in this páramo that correspond to the plant forms predicted. Non-native but well naturalized taxa are shown in parentheses, e.g. *Rumex acetosella*. Question marks indicate missing information or, for particular taxa, unknown occurrence or naturalization status. Barely occurring, perhaps only at lower elevation, are small evergreen shrubs of *Vaccinium floribundum* or *V. meridionale*, which in the model are almost precluded by warmth criteria. (All summergreen forms are precluded by the small annual temperature variation.) Despite the mostly moist conditions year-round, the predicted vegetation in this alpine climate must be interpreted as a somewhat open scrub of shrubs, bunch and tussock grasses, plus the taller but more scattered tuft arborescents.

Matches of plant taxa to particular plant forms were determined from information available on the Internet (especially from Luteyn, no date) and from two páramo visits, the latter with field assistance by Alejandro Velázquez. Species names are as used at the time and place; lichen names are from Pérez (1987), Sipman (2002) and other references therein.

Páramo de Piedras Blancas, Venezuela		8.85°N, 70.80°W, 4150m	
T	2.7 3.6 4.4 4.0 3.4 2.8 2.6 2.9 3.5 3.4 2.8 2.4	3.2°C, Tabmin = -11.0°C (estd.)	
P	6 21 55 98 147 187 136 81 39 21 40 19	850 mm	
BT = 3.2, MIY = 1.65, PETy = 514 mm			
A	+Tropical Alpine Tuft-Arborescents	Tabmin	.09 <i>Espeletia timotensis</i> , <i>E. moritziana</i> , <i>E. spicata</i>
S	Cool-Evergreen Small Shrubs	Tmax	.03 <i>Hypericum laricifolium</i> , <i>Stevia lucida</i> , <i>Vaccinium?</i>
DS	EG Polar/Alpine Dwarf Shrubs EG/semi-EG Cushions	Tmin	.02 <i>Hinterhubera imbricata</i>
		Tmin	.03 <i>Azorella julianii</i> (herbaceous)
G	+ Short Tussock Grasses Short Bunch Grasses (graminoids)	Tmin	.12 <i>Muhlenbergia ligularis</i> , <i>Trisetum (?)</i>
		Tmax	.19 <i>Agrostis breviculmis</i> , <i>A. trichoides</i> , <i>Aegopogon</i> ; <i>Luzula racemosa</i>
F:	+ Perfrigid Quasi-EG Forbs + Frigid Cushions Semi-Evergreen Forbs	Tmin	.20 <i>Castilleja</i> , <i>Gnaphalium</i> , <i>Lupinus</i> , <i>Senecio</i> (<i>Rumex acetosella</i>)
		Tmin	.20 <i>Arenaria muscifolia</i> , <i>Aciachne pulvinata</i> , <i>Lucilia venezuelensis</i>
		Tmax	.03 <i>Acaena cylindrostachya</i> , <i>Calandrina acaulis</i> , <i>Hypochoeris setosus</i>
Th	Mat-Forming Thallophtyes Xeric Thallophtyes	Mly	.34 <i>Polytrichum</i> , <i>Hypnum</i> ; <i>Lycopodium reflexum</i>
		Tmax	.43 <i>Thamniola vermicularis</i> , <i>Megalospora foersteriana</i> , <i>Oropogon</i> , <i>Hypotrachyna</i> , <i>Cetrariastrum</i>

Table 6. Predicted PFORMS Model Results for Forty Mile Scrub.

Forty Mile Scrub is a protected area in north-central Queensland (Australia), where the climate is tropical wet-dry, and the natural vegetation is a variably open, semi-evergreen woodland dominated by a mix of raingreen and sclerophyll trees and arborescents. This vegetation was called “dry rainforest” by Fensham (1996).

The left-hand column shows the plant forms predicted for this site by the PFORMS model, listed by plant structural type (see Table 2 for key to table contents and abbreviations). Topo-specific forms are shown in brackets. The closest limiting factor in the envelope design is shown in the third column (e.g. MIy for moisture index), followed by the relative proximity to closest envelope limit (u = upper value limiting).

The right-hand column shows plant taxa occurring in this area that correspond to the plant forms predicted. Non-native but perhaps well naturalized taxa are shown in parentheses; probably not naturalized but widely planted ornamental taxa are shown in brackets. Question marks indicate missing information or, for particular taxa, unknown occurrence or naturalization status. With an annual moisture balance (MIy) of 0.67, this prediction can be interpreted as a semi-evergreen woodland, in which sunlight reaches the ground commonly as frequent sunflecks (cover perhaps about 60%).

The largest error in climate-based models of Australia is the prediction of stem-succulents, which did not occur in the native flora (except *Sarcostemma*). In addition, no [predicted] Leaf-Succulent or distinctly Mediterranean Evergreen Shrubs, or Xeric Cushion or Summergreen Forbs, could be identified with any certainty; and Raingreen Arborescents may be represented only by immature potential trees. Not predicted but found were *Parsonsia* (an evergreen liana), epiphytic *Dendrobium linguiforme*, and evergreen *Crinum* (forb, probably evergreen).

Matches of plant taxa to particular plant forms were determined (assisted greatly by Andy Gillison) from notes taken on one field visit, plus information available on the Internet (e.g. Dept. Env. Sci., no date), and from Fensham (1996), Prior & al. (2003, 2004), and Williams & al. (1997). Lichen names were from Archer and Elix (2017) and Sipman (2018).

Forty Mile Scrub (climate ex Mt Surprise), Australia		18.10°S, 144.85°E, 780m	
f	25.2 24.6 23.8 21.8 19.1 16.8 16.1 17.7 20.7 23.8	25.5 25.9	21.7°, Tabmin = -0.2° (estimated)
P	244 216 94 30 20 6 1 7 5 16	59 103	800mm
BT = 21.7, MIy = 0.62, PETy = 1283mm			
T:	Xeric Raingreen Trees	MIy	0.22 <i>Pleiogynium timorense</i> , <i>Gyrocarpus americana</i> , <i>Planchonnia careya</i> , <i>Ailanthus triphysa</i> , <i>Eucalyptus alba</i>
	Tall Sclerophyll Trees	MIy	0.10 <i>Eucalyptus crebra</i> , <i>Eu. tereticornis</i> , <i>Eu. mollucana</i>
	Bottle Trees	Tmax	0.06 <i>Brachychiton australis</i> (deciduous)
	Tropical EG Microphyll Trees	MIy	0.02 <i>Alectryon connatus</i> , <i>Dysoxylon oppositifolium</i>
	Tropical Coriaceous EG Trees	MIy	0.02 <i>Ficus obliqua</i>
	Tropical Xeric Needle Trees	MIy	0.02 <i>Casuarina</i>
ST:	Raingreen Small Trees	MIy	0.30 <i>Flueggea</i> spp. [<i>Melia azedarach</i>]
	Trop-Evergreen Small Trees	MIy	0.02u <i>Geijera salicifolia</i> , <i>Analaya hemiglauca</i> , <i>Strychnos psilosperma</i> , <i>Nastelaea microcarpa</i> , <i>Austrorivinus</i> , <i>Drypetes deplanchei</i> , <i>Acacia</i>
	Dwarf-Needle Small Trees	Tmin	0.14 <i>Callitris intratropica</i> ; <i>Citriobatis spinescens</i> (leptophyll)
RT	Bottle Palms	MIy	0.01u <i>Hyophorbe lagenicaulis</i>
A	Raingreen Arborescents	MIy	0.44 ???
	Sclerophyll Arborescents	MIy	0.30 <i>Eucalyptus shirleyi</i> , <i>Eu. persistens</i> , <i>Eu. exserta</i> ; <i>Acacia</i> spp.
	Xeric EG Tuft Arborescents	MIy	0.31u <i>Xanthorrhoea</i> ? (seen nearby but not on local species lists)
	Xeric Stemgreen Arborescents	MIy	0.14 ???
S	Tropical Evergreen Shrubs	MIy	0.02u <i>Diospyros humilis</i> , <i>Erythroxylon</i> , <i>Petalostigma banksii</i> , <i>Carissa ovata</i> , <i>Denhamia obscura</i> , <i>Phyllanthus</i> ?
	Leaf-Succulent Shrubs	Tabmin	0.06 ???
	Mediterranean EG Shrubs	Tmin	0.14 ???
DS	Xeric Semi-Shrubs	MIy	0.23 <i>Waltheria indica</i> , <i>Abutilon oxycarpum</i> , <i>Hibiscus</i> , <i>Sida</i> , <i>Solanum</i>
RS	Xeric Rosette-Shrubs	MIy	0.45 (no natives: rosette forms all mesomorphic)
SS	Tall-Column Stem-Succulents	MIy	0.23
	Arboresc. & Frutesc. Stem-Succulents	MIy	0.47u [<i>Opuntia</i>]
	Cryptic Stem-Succulents	MIy	0.31
G	Tall Grasses	MIy	0.02 <i>Heteropogon triticens</i>
	Short Bunch Grasses	MIy	0.35u <i>Themeda</i> , <i>Heteropogon contortus</i> , <i>Chloris truncata</i> , <i>Microlaena stipoides</i>
	Desert Grasses	MIy	0.06 ???
F	Raingreen Forbs	MIy	0.35u <i>Centrolepis exserta</i> , <i>Lomandra</i> (both with rolled lvs)
	Xeric Cushion Forbs	MIy	0.35 ???
	Succulent Forbs	Tabmin	0.23 [<i>Portulaca oleracea</i>]
	Summergreen Forbs	Tmin	0.07 ???
Fn	Raingreen Ferns	MIy	0.30 <i>Cheilanthes</i> ? <i>Doryopteris</i> ? <i>Paraceterach muelleri</i> ? <i>Pyrrhosia rupestris</i> ?
V	Raingreen Vines	MIy	0.30 <i>Clematis pickeringii</i> , <i>Ipomoea gracilis</i> , <i>Cucumis</i> ? <i>Pandora pandorana</i> ?
	Evergreen Vines	MIy	0.02 <i>Cissus oblonga</i> , <i>Cassythia filiformis</i> , <i>Sarcostemma viminalae</i> ssp <i>brun.</i>
E	Wintergreen Bush Epiphytes	MIy	0.30 <i>Viscum articulatum</i> , <i>V. whitei</i> ssp <i>whitei</i>
Th	Mat-Forming Thallophytes	MIy	0.02 <i>Archidium rothii</i> , <i>Ptychomitrium australe</i>
	Xeric Thallophytes	MIy	0.50 <i>Pertusaria glebulosa</i> , <i>P. trimera</i> , <i>Parmotrema</i> , <i>Graphina</i>

Conclusion and Next Steps

This paper suggests a method for evaluating one kind of non-floristic vegetation model with floristic data, by using as intermediary the basic ecological plant types that compose the vegetation and which can be matched with actual species. This is a demonstration, and is not intended as an attempted or even implied model validation, which would require a large set of well distributed, geographically representative data sites and their field data. The above results, therefore, represent only a demonstration of how a fairly rigorous evaluation of general vegetation models could be done, with available data. There are a few gaps in the evaluation tables herein, but these missing (or incorrect) mismatches of plant forms to species do not alter the value of the above as a potential evaluation methodology.

Models should be validated, but this is not always done. The lack of rigor in model evaluation, or even of attempted evaluation, has been criticized perhaps most eloquently in the useful book *A Critique for Ecology* (Peters 1991). The validation problem was once central to ecological model building (e.g. Goodall 1972; Caswell 1976; Overton 1977; Holling 1978) and resulted in at least two main concepts: verification (does the model produce the intended results?) and validation (would the model work anywhere within its specified range?) (see summary by Rykiel 1996; cf Rastetter 1996; Power 1993). This last test, i.e. validation, is much more rigorous and is generally considered to require testing of model results against independent data, i.e. data not used in building the model. Unfortunately, the need for validation seems to be largely discarded nowadays as unnecessary for publication.

Few if any such treatments, however, have considered *geographic* models seriously, i.e. beyond superficial “kappa statistics”. But global and other large-area models are inherently geographic models, and should be validated geographically, i.e. in all the main geographic and physiographic regions in which such models are to be used (Box & Meentemeyer 1991). The first version of this climatic-envelope model was described as having “stood up to testing” (Peters 1991, p. 284), but in reality, even a moderate evaluation of a global model would require testing at several hundred sites worldwide, representing the world’s main climatic types and subtypes, and their different regional occurrences (see appendix in Box 2016). Since we have only one Earth, validation with independent data has generally been considered impossible, but suggestions have been made (e.g. Rastetter 1996).

Climatic-envelope models demonstrated climatic control of the geographic ranges of different general plant types. They also demonstrated what could be predicted with widely available climatic data and a global perspective, even in the early 1980s; and provided a means of generating and testing hypotheses or other questions of plant-environment relationships. This is especially true of PFORMS, which can be applied at any climatic site and which contains an order of magnitude more plant types than do most other models. Evaluation of predictive models for plant types, as demonstrated here, requires thinking in two directions:

- 1) What local examples (species) occur for the plant forms predicted?
- 2) To what forms (predicted or not) do the main species belong?

These criteria permit identifying not only successful predictions but also errors,

both of omission and commission. Improvement and true evaluation of global vegetation models requires extensive field experience and data from most parts of the world, with results published as a monograph or book.

Formal evaluation of PFORMS must also await always ongoing revisions of plant types, climatic limits, and inclusion of more integrative variables, such as durations of favorable conditions, as suggested by the world climatic classification system of Lauer and Rafiqpoor (2002). There are of course many concepts of vegetation types and other (i.e. non-envelope) types of vegetation models. Models with vegetation types conceived as opaque “blocks” (e.g. Emanuel & al. 1985; Prentice & al. 1992) probably cannot be evaluated using floristic data. But types with some conceptualization of internal structure, such as main structural elements or more numerous main constituent plant types, can be evaluated rigorously by matching species and plant types, based on their morphological characters.

Finally, one of the biggest problems with species-based methodologies, phytosociology in particular, is that the resulting syntaxonomical names, for example a *Corylo heterophyllae-Quercion mongolicae*, are difficult, may be confusing, and may only be understood completely by people familiar with the scientific names in the local or regional flora (cf Rejmánek 1997). Phytosociology consists of three steps: collection of field data, tablework, and syntaxonomy, i.e. the placement of identified species clusters (communities) into an overall global hierarchy. This last step is the weakest, not only because it is often opaque, but also because it follows rules of correctness and priority rather than substance (Ewald 2003), and because there is no overall control on inflation of meanings or on unlimited proliferation of names (e.g. Pignatti 1968, 1995; Pignatti & al. 1995; Loidi 2020). These problems might be addressed with some success by wider but formalized use of parallel names using normal words, for example “beech-oak forest”, or *Fagus-Quercus* forest, as a formally defined synonym for the phytosociological unit *Querco-Fagetum*. Rigorous parallel but quite different naming might also force decisions on the validity of different but overlapping or otherwise similar phytosociological units, thus reducing their overall redundancy and attendant confusion to a wider scientific audience.

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