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# Dynamic endemism and 'general' biogeographic patterns

BY SILVIO SHIGUEO NIHEI

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This paper deals with some theoretical aspects of areas of endemism. I do not intend to make a contribution toward an innovative methodology but, in fact, my major concern is toward understanding and approaching areas of endemism under a dynamic view, which I am terming 'dynamic endemism'. Following my initial argumentation on dynamic view of areas of endemism, I will thereafter exemplify my discussion with two case studies (Amazonia and the Mexican Transition Zone).

Areas of distribution and areas of endemism are understood as basic elements in biogeography. Area of distribution can be defined as the whole spatial range occupied by a taxon at a given time (Roig-Juñent et al. 2002) or a region occupied by a monophyletic taxon (Humphries and Parenti 1999). Basic information in biogeography are the localities of occurrence known for a given taxon, and gathering of localities is the starting point for the inference of areas of distribution. As it is virtually impossible to have all the localities of occurrence known and recorded for any taxon, some manual methods have been applied by authors to estimate area of distribution by extrapolation (see Roig-Juñent et al. 2002 for a review). On the other hand, definition of areas of endemism is considerably more complex. Many authors have approached the subject with both theoretical and operational discussions (Nelson and Platnick 1981, Cracraft 1985, Harold and Mooi 1994, Morrone 1994, Linder 2001, Roig-Juñent et al. 2002, Hausdorf 2002, Szumik and Goloboff 2004). Nevertheless, some common points can be traced among the several authors and, despite differences and controversies, in a general way, areas of endemism can be defined in terms of spatial coincidence among areas of distribution of different taxa. For a comprehensive definition we can refer to that of Harold and Mooi (1994), by which areas of endemism should be recognized after phylogenetic and distributional congruence: "...area of endemism as a geographic region comprising the distributions of two or more monophyletic taxa that exhibit a phylogenetic and distributional congruence and having their respective relatives occurring in other such-defined regions" (Harold and Mooi, 1994 p. 262).

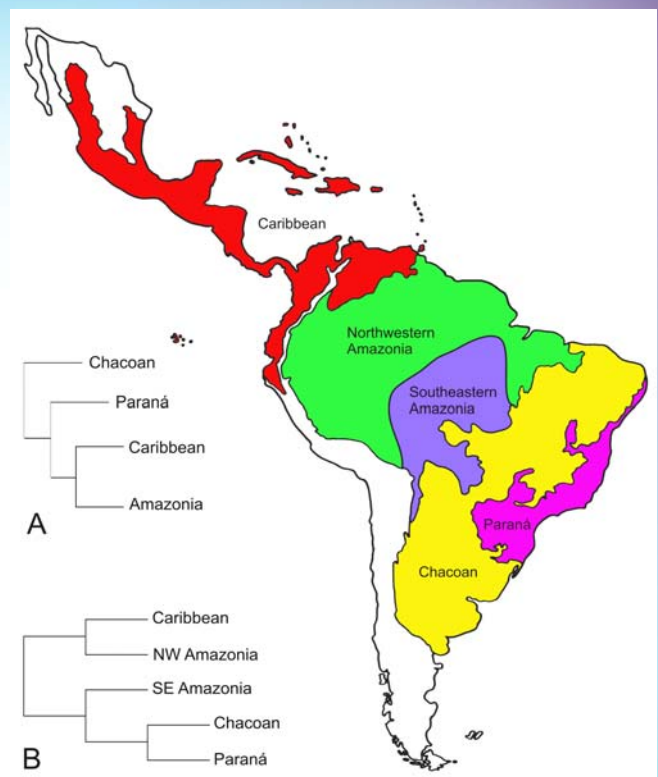
Coincidence on biotic history (phylogeny) and on their distribution in space should thus be regarded as the main components assumed as relevant and essential to recognize areas of endemism. The complexity on dealing with areas of endemism is that identification (delimitation) of areas of endemism and the area relationships reconstruction are two inextricable steps. Morrone (2001b) defined this as being a two-stage analysis comprised first by the recognition of areas of endemism (primary biogeographic homology) and then a cladistic test of the previously recognized areas (secondary biogeographic homology). That is a rational procedure intended to integrate panbiogeography (to identify primary spatial homologies) and cladistic biogeographic methods (to evaluate and legitimate the previously identified homologies). Since areas of endemism are hierarchically linked (nestedness) and scale-dependent (Cracraft 1985), when defining area relationships one is also delimiting the areas of endemism in a given scale. Therefore, an area may be a set of localities on southeastern Brazil at one end to the Neotropical region at the other end, or even Gondwana and Pangaea, if going back to past areas. This reciprocal dependence raises another problem towards a reliable delimitation of areas of endemism, because the cladistic test (*sensu* Morrone 2001b) results in relationships among areas of endemism and therefore secondary biogeographic homologies are recognized and evaluated in a given hierarchical level (above-terminals) but without considering the monophyly of those terminals.

An area of endemism is a biological concept of space that contemplates processes and pattern. Processes related to the recognisability of areas of endemism are of two basic kinds, *geological* spatio-temporal processes (plate tectonics, climate change, sea water level change, etc.) and *biological* spatio-temporal processes (vicariance and extinction). Exemplification of this argument follows as 'Stage 1' (the processes): areas of endemism should exist due to intrinsic response of an ancestral taxon affected by the presence of a geological/ abiotic barrier splitting its original distribution, and the response (vicariance) being the isolation of that ancestral and subsequent differ-

entiation into two derived sister-taxa. And 'Stage 2' (the pattern): when there is coincidence of several different taxa presenting the same vicariant response to that exactly same geological/ abiotic barrier, so there is a biogeographic pattern recognizing areas of endemism and their relationship. Similar responses from different taxa to the same geological events generate a congruent pattern of area relationships (spatial and temporal congruence, *sensu* Donoghue and Moore 2003). In a higher-level perspective, we might observe nestedness of restricted areas of endemism (districts and provinces) into large-scale areas of endemism (subregions, regions and realms) as Amazonia, the Atlantic Forest and the Neotropical region. Morrone (2001b) pointed out this as a "natural hierarchy of the biogeographical system".

Within a given time range ( $\Delta t$  between  $-10$  and  $-7$ , assuming  $t=0$  as the present time), a given area will involve a series of geological/ abiotic events. Similar responses from different taxa at this  $\Delta t$  will generate a general biogeographic pattern X. In another time range ( $\Delta t$  between  $-6$  and  $-3$ ), the same area will involve another series of geological events, and again, similar responses from different taxa at this  $\Delta t$  will generate another general biogeographic pattern Y. Patterns X and Y might be similar or not in terms of area relationships. Even in case of similarity, they are not congruent, as they were resulting from different series of geological events, thus temporally incongruent. Assuming that in the pattern X the areas A-B-C-D-E have resulted with the relationship (A(B(C(D,E))))), and in pattern Y related as (A((C,E)(B,D))). Based on this, one may conclude that DE is an area of endemism (monophyletic) in X, but not in Y. This illustrates how areas of endemism have their 'existence' affected along time scale and the floating dynamics of endemism across temporal dimension. This hypothetical explanation and my initial argumentation on dynamic endemism could be exemplified by some study-cases but herein I will discuss two important and relatively well-studied areas: Amazonia and the Mexican Transition Zone.

Amazonia is a spatial unit traditionally regarded as a historical unit (Fig. 1A), which means that biotic elements from all the small inclusive units of Amazonia share a common history. Several studies have supported Amazonia as a biogeographical unit: on Reduviidae bugs (Morrone and Coscarón 1998), primates (Da Silva and Oren 1996), passerines (Bates et al. 1998), several plant and animal taxa (Morrone 2000, 2001a), and many others. On the other hand, there are also several studies with favourable evidence on the hypothesis that Amazonia is a composite area (Fig. 1B): on primates and Nematoceran flies (Amorim and Pires 1996, Roig-Juñent and Coscarón 2001), Brachyceran flies (De Carvalho 1999, De Carvalho et al. 2003, Nihei and De Carvalho, 2007), Meliponini bees (Camargo



**Fig. 1.** Biogeographical classification of the Neotropics into subregions as suggested by Nihei & De Carvalho (2007), with area relationships proposed by: A, Morrone and Coscarón (1998); B, Nihei and De Carvalho (2007).

1996, Camargo and Moure 1996, Camargo and Pedro 2003), Pentatomiidae bugs (Grazia 1997), Cercopidae homoptera (Goldani and Carvalho 2003), Curculionidae beetles (Morrone 2002), Riodinidae butterflies (Hall and Harvey 2002), Trichodactylidae decapods (Morrone 2003), Felidae mammals (Eizirik et al. 1998), Aves (Cracraft and Prum 1988, Prum 1988, Marks et al. 2002), *Cecropia* plants (Franco and Berg 1997), several plant families (Cortés and Franco 1997), and several plant and animal taxa (Morrone 2000).

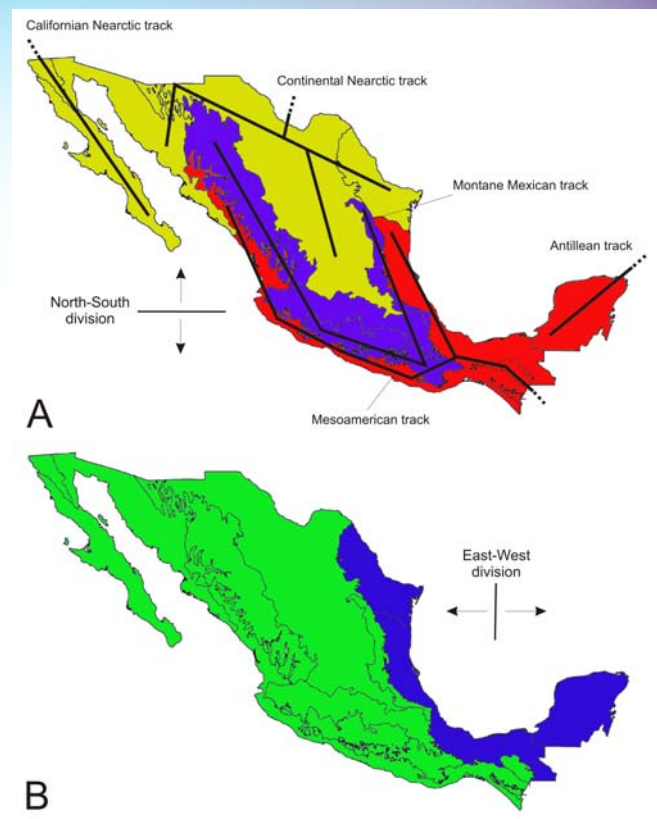
Not all of these individual patterns can be gathered within the same general pattern, however, because these patterns are not temporally congruent (Nihei and De Carvalho 2007). Ages provided by authors were Cretaceous (Amorim and Pires 1996, Grazia 1997, De Carvalho 1999), Quaternary (Manfrin et al. 2001), Cenozoic (Cracraft and Prum 1988), and Pliocene-Pleistocene (Eizirik et al. 1998). Furthermore, the Platyrrhini monkeys included in the pattern of Amorim and Pires (1996), besides the Nematoceran dipterous, have been dated to Oligocene (35 mya) (Schrágo and Russo 2003). The hypothesis of composite Amazon was first developed by Dalton Amorim and Maria Rita Pires (Amorim and Pires 1996, Amorim 2001) and the main geological event responsible for generating that pat-

tern is the lacustrine formation in Amazon basin along the Amazonas-Madeira-Mamoré rivers caused by marine water transgression during Late Cretaceous. Nevertheless, several studies have reinforced that marine water transgression into the South American continent has taken place several times in the past (Hooen 1993, Räsänen et al. 1995, Frailey 2002, Nores 2004, etc.), not only during the Late Cretaceous as pointed out in the model. And that is why this same pattern could be observed repeatedly in different groups on different time periods, leading some authors to equivocally determine a general biogeographic pattern, when in fact they are dealing with “pieces of different puzzles” (Nihei & Carvalho 2007).

Part of the discordance on the status of Amazonia as a unit or a composite area might be related to this temporal dynamism on the existence of a vicariance event dividing the Amazon. Organisms that did not respond or were not affected by the marine water transgression forming an epicontinental sea in Amazon do have corroborated a biogeographical pattern showing Amazon unity, as corroborated by the references aforementioned. While the organisms affected by this epicontinental sea, whenever it have occurred, have corroborated a pattern with Amazon as a composite area.

My second example is the Mexican Transition Zone (Fig. 2). This transitional area interfaces Neotropical and Nearctic regions and was firstly recognized and discussed by Gonzalo Halffter (1962, 1976, 1978, 1987). Besides, several studies have undertaken biogeographic analysis of this area (Liebherr 1994, Hernández-Baños et al. 1995, Luna-Vega et al. 1999, Marshall and Liebherr 2000, Morrone and Márquez 2001, Escalante et al. 2007, and several others; see Morrone 2005 for a review). Despite differences on the delimitation of areas of endemism and discordances on the areas relationships, we can synthesize a common finding recognized by the different authors. A number of the proposed area relationships converge so that Mexico is divided along the Transmexican Volcanic Belt into one northern and other southern portions (e.g., Liebherr 1994, Marshall and Liebherr 2000, Morrone and Márquez 2001) (Fig. 2A). A recent study (Escalante et al. 2007), however, has revealed an opposite hypothesis with a division into eastern and western portions partially delimited, at the present time, by the mountain range of Sierra Madre Oriental (Fig. 2B). Escalante et al. (2007) distinguish both divisions by the age and nature of the major geological event responsible for generating each pattern: the north-south division due to North and South American plates convergence on Miocene period, whereas the east-west division associated to the Caribbean plate eastward migration in the Paleocene.

The Mexican Transition Zone is widely and unquestionably recognized as a complex area with compos-



**Fig. 2.** Biogeographical classification of Mexico into provinces based on Morrone (2001a, 2004) (modified from Morrone 2005), with indication of: A, North-South division (Morrone and Márquez 2003); B, East-West division (Escalante et al. 2007).

ite biotic nature, with not only Nearctic, Mesoamerican and South American affinities of its inhabiting biota, but also particular endemism. With regards to the attributes and differences between each area, some parallels can be made by extending the discussion on the dynamism of Amazonian biogeography to the Mexican Transition Zone. In this second case, we also observe dynamic patterns of endemism, with dual area cladograms recognizing relationships differing according to the temporal dimension (Paleocene or Miocene). Escalante et al. (2007) have assumed that former studies have not detected these two opposite patterns on the area, perhaps some of them comparing (and even constraining) the distributional patterns obtained onto the existing hypothesis of north-south division. The authors correctly warn that “previous biotic diversification studies of the Nearctic and Neotropical regions need to be revised”.

By assuming this view, one should define and delimit spatial homologies (areas of endemism) also incorporating temporality. For this reason, methods available to identify primary spatial homologies (e.g., panbiogeography, PAE, NDM) are not questioned herein, except that their users must be aware of the

temporal dynamics of areas of endemism. Additionally, general biogeographic patterns for any area should incorporate temporal dimension and be interpreted as age-based patterns and not only form and space-based patterns. Area-relationships might differ along the time and obviously patterns also should be different and interpreted as differing for any time interval. Under this perspective, we should understand biogeographic general patterns as general hypothesis associated to a given time interval and not as an atemporal general hypothesis.

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**Silvio Shigueo Nihei**  
**Departamento de Zoologia, Instituto de Biociências,**  
**Universidade de São Paulo, Rua do Matão, Travessa**  
**14, n.101, Cidade Universitária, São Paulo-SP, 05508-**  
**900, Brazil.**  
**e-mail: silvionihei@gmail.com**

# De los modelos de nicho ecológico a las áreas de distribución geográfica

POR PATRICIA ILLOLDI-RANGEL Y TANIA ESCALANTE

En los últimos diez años se ha observado un avance vertiginoso en el desarrollo de algoritmos que permiten modelar el nicho ecológico de las especies. Los modelos de nicho ecológico se han utilizado para una gran variedad de aplicaciones, que incluyen desde la cuantificación del nicho ecológico de una especie en particular, hasta la evaluación del efecto de los cambios climáticos y la deforestación sobre la biodiversidad (para una revisión ver Guisan y Thuiller 2005). El uso más frecuente de estos modelos en biogeografía es como predicciones o modelos del área de distribución geográfica de un taxón, los cuales pueden usarse para identificar posteriormente patrones biogeográficos, tales como los que conducen a proponer regionalizaciones biogeográficas. Un modelo de distribución de especies relaciona las observaciones realizadas en campo de los taxones con variables ambientales (Guisan y Zimmermann 2000). Estas relaciones entre las especies y el ambiente pueden causar diferentes patrones espaciales, observables a diferentes escalas. Este tipo de datos, derivados de las relaciones, son manipulados más adecuadamente a través de un Sistema de Información Geográfica (SIG), herramienta que también se ha desarrollado en las últimas décadas y que ha tenido gran influencia en el desarrollo del modelamiento de los nichos y de las áreas de distribución.

Aquí analizamos las aplicaciones de los modelos de nicho ecológico para ser inferidos como áreas de distribución potencial, sus limitaciones y las perspectivas que ofrece su uso en biogeografía.

## Biogeografía ecológica e histórica y su integración

De acuerdo con Ruggiero y Ezcurra (2003), el análisis de las áreas geográficas, en particular los de las zonas de transición, es estudiado con un enfoque claramente cuantitativo por parte de los biogeógrafos ecólogos, mientras que para los biogeógrafos históricos esta orientación es más bien cualitativa. Recientemente se ha propuesto que las subdisciplinas que conforman a

la biogeografía, llamadas biogeografía ecológica e histórica, deberían integrarse en una sola aproximación donde los patrones que se identifican y sus procesos subyacentes deben ser incorporados (Crisci et al. 2006, Escalante 2007, entre otros), puesto que tanto los procesos históricos como los ecológicos están operando simultáneamente. Pero, ¿cómo hacerlo? Una forma de integrar ambos aspectos de la biogeografía es a través del uso de los modelos de nicho ecológico de los taxones aplicados en metodologías históricas, por ejemplo en biogeografía cladística (v. gr. Wiens y Donoghue 2004, Wiens y Graham 2005) y en la identificación de áreas de endemismo, combinados con los métodos del Análisis de Parsimonia de Endemismos (PAE; Morrone 1994) (v. gr. Rojas-Soto et al. 2003, Escalante et al. 2007) y el método de optimización de áreas de endemismo (Szumik et al. 2002, Szumik y Goloboff 2004). También podrían ser útiles para identificar zonas de transición, al mejorar los datos básicos utilizados en índices biogeográficos y en la caracterización de nodos panbiogeográficos. Sin embargo, el uso actual casi indiscriminado de los modelos de nicho ecológico nos lleva a preguntarnos qué es en realidad un modelo de nicho ecológico y por qué es que puede ser usado para inferir áreas de distribución potencial y patrones biogeográficos (tales como los gradientes de riqueza, el endemismo y la disyunción).

## El nicho ecológico

Si queremos referirnos al modelado de especies, debemos definir, en primera instancia, el concepto de nicho. Éste incluye a todos los factores bióticos y abióticos con los cuales cualquier organismo se relaciona, en un tiempo y espacio determinado. Formalmente, el nicho ha sido descrito como un hipervolumen de  $n$ -dimensiones, donde cada dimensión corresponde a uno de los factores antes descritos. De esta forma, el nicho involucra a todos los recursos presentes del ambiente, las adaptaciones de los organismos y cómo se relacionan éstos dos, *sensu* Grinnell (1917) o

Hutchinson (1957). Este concepto general de nicho puede ser delimitado a lo que ha sido llamado nicho ecológico, en donde hace referencia al tiempo actual en el cual se desarrolla el organismo, y cómo éste interactúa con los factores ambientales que lo rodean. Para una discusión más extensa del concepto de nicho ver Peterson (2006).

## Modelos de nicho ecológico

En general, en la literatura son a menudo usados indistintamente los nombres "modelos de nicho ecológico" y "modelos de distribución", e incluso conceptualmente pueden ser muy semejantes. Los modelos de nicho ecológico son modelos usados para desarrollar relaciones entre los valores ambientales y los datos de presencia, presencia-absencia y/o abundancia conocidos de las especies (Graham et al., 2004). Por otro lado, los modelos de distribución de especies son modelos que relacionan las observaciones de campo de los taxones con variables ambientales predictivas, basadas en una respuesta estadística o teórica (Guisan y Zimmermann 2000, Guisan y Thuiller 2005). Sin embargo, aunque parecen lo mismo, pensamos que existe una diferencia, aunque sutil, entre ambos conceptos (ver más abajo).

Los modelos de distribución de especies, utilizando el nicho ecológico como base teórica, son herramientas muy útiles para resolver preguntas de ecología aplicada, conservación y biogeografía, debido a las bases ecológicas y evolutivas subyacentes (Guisan y Thuiller 2005). Se han desarrollado varios modelos que ayudan a comprender algunas de las dimensiones ambientales y ecológicas en las que se encuentra un taxón, principalmente aquellas relacionadas con factores abióticos (precipitación, temperatura, entre otras) y bióticos (tipos de vegetación en las cuales se puede encontrar). El desarrollo de algoritmos matemáticos permite, cada vez más, modelar con mayor precisión el nicho ecológico de los taxones. Entre los diferentes algoritmos de modelado que existen, podemos mencionar principalmente a BIOCLIM (Busby 1991), GARP (Stockwell y Peters 1999) y Maxent (Phillips et al. 2006). Cada uno de ellos presenta un acercamiento diferente al problema del modelado del nicho ecológico, ya sea a partir del uso de algoritmos de envolturas climáticas (BIOCLIM), de algoritmos genéticos (GARP) o de algoritmos de máxima entropía (Maxent).

## Algoritmos para modelar nichos ecológicos

BIOCLIM utiliza lo que se denomina envoltura climática (*climatic envelop*) para encontrar una regla única que identifique todas las áreas con clima similar al de la

localidad de las especies. El algoritmo básico de BIOCLIM (Nix 1986, Busby 1991, McMahon et al. 1996) encuentra el intervalo climático en el que se encuentran los puntos para cada variable climática involucrada en el análisis. Las suposiciones principales utilizadas en modelos de envoltura climática son: (1) la distribución de las especies está determinada por el clima, (2) la distribución estadística de las variables climáticas es normal, y (3) todas las variables con intervalos restringidos influyen a la especie de interés.

GARP (Genetic Algorithm for Rule-set Prediction, por sus siglas en inglés) utiliza un algoritmo genético para la búsqueda de asociaciones entre variables ambientales y la ocurrencia conocida de las especies, contrastándola con las características ambientales a lo largo de toda el área de estudio. El algoritmo remuestra automáticamente los datos para crear una población de 1250 puntos de presencia. Un número equivalente de puntos se remuestra en el resto del área de estudio, en donde la especie no ha sido registrada. Esto crea un total de 2500 puntos que serán utilizados para realizar los modelos y validarlos (Peterson y Nakazawa 2008). Una vez realizado esto, el algoritmo elabora modelos diferentes con las reglas elegidas (atómicas, de intervalos, de intervalos negados y de regresión logística) hasta alcanzar un número determinado de iteraciones (repeticiones de las reglas) o alcanzar un determinado límite de convergencia, es decir, cuando ya no se modifique la precisión de la predicción a partir de nuevas adiciones. Los modelos de nicho ecológico finales serán entonces proyectados en el espacio geográfico como mapas digitales. Este método ha sido ampliamente aplicado en la predicción de la distribución de especies de animales y plantas (v. gr. Peterson et al. 2002a, b, Illoldi-Rangel et al. 2004, Thomas et al. 2004, Araújo et al. 2005, Thuiller et al. 2005). El uso de modelos generados en GARP presenta una serie de beneficios: (1) permite la determinación cuantitativa de probabilidades de cualquier dato, incluyendo aquellos datos únicamente de presencia (i.e. registros de museos); (2) se añade valor al escaso muestreo que existe para algunas especies al incrementar la cobertura y resolución; y (3) permite producir modelos de fácil comprensión basados en reglas para explicar relaciones entre los datos (Peterson y Nakazawa 2008).

Maxent está fundamentado en el concepto de máxima entropía, utilizando una aproximación mecanicista para realizar predicciones a partir de información incompleta. Maxent estima la distribución más uniforme (de ahí el concepto de máxima entropía) a lo largo del área de estudio con la restricción de que el valor esperado para cada variable ambiental en una distribución concuerda con su promedio empírico (valores promedio para el conjunto de datos de ocurrencia) (Phillips et al. 2004, 2006). Maxent pesa cada característica (variable ambiental) al multiplicarla por una



constante, y la divide posteriormente para asegurar valores de probabilidad entre 0 y 1. El programa inicia con una distribución uniforme de probabilidades e iterativamente altera el peso de una variable a la vez para maximizar la similitud de los datos de ocurrencia. El algoritmo está garantizado para converger en la distribución probabilística óptima, y dado que no aleatoriza, los resultados son determinísticos. Las predicciones de Maxent para cada celda analizada hacen referencia a valores acumulativos, representando como porcentaje el valor de probabilidad para la celda en cuestión y todas aquellas con valores iguales o menores de probabilidad. Una celda con valor de 100 es la más adecuada, mientras que celdas con valores cercanos a 0 son las menos adecuadas dentro del área de estudio (Phillips et al. 2004).

### La proyección hacia el área de distribución geográfica

Una vez que se han generado los modelos, bajo cualquier algoritmo que se seleccione, es necesario proyectarlos a lo que se define como el área de distribución geográfica potencial, o simplemente área de distribución potencial. Este paso no es trivial. Es necesario aclarar entonces el concepto de área de distribución antes de continuar: un área de distribución es la superficie geográfica ocupada por un taxón, con la que interactúa de manera no efímera, y se construye a partir de las localidades donde se ha registrado (Espinosa et al. 2001, Zunino y Zullini 2003). El área de distribución potencial será la inferencia acerca de cuál es el área de mayor probabilidad en la que un taxón esté presente (Espinosa et al., 2001). Los factores que determinan entonces que una especie se encuentre en un área determinada son (Soberón y Peterson 2004): (1) las condiciones abióticas (incluyendo al clima, ambiente físico, condiciones edáficas, etc., en general aquellos factores que limitarían fisiológicamente la sobrevivencia de un taxón en un área); (2) los factores bióticos (interacciones con otras especies que modifican la capacidad de mantener poblaciones); (3) la dispersión hacia áreas accesibles dependiendo de la vagilidad de cada taxón; y (4) las capacidades evolutivas de las poblaciones para adaptarse a nuevas condiciones. Además, nosotras incluiríamos: (5) los procesos de extinción; (6) la presencia de barreras geográficas, relacionadas con eventos vicariantes; y (7) los procesos de especiación (Fig. 1).

Dado lo anterior, un modelo de nicho ecológico puede estar sobrerrepresentando el área de distribución geográfica de una especie, dado que en el modelo se están considerando todos aquellos sitios en donde se encuentran las mismas condiciones ecológicas bajo las cuales se registraron originalmente los pun-

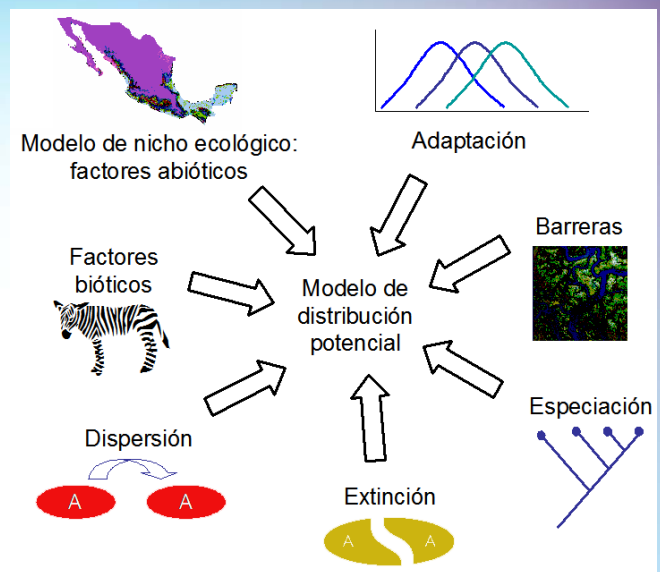
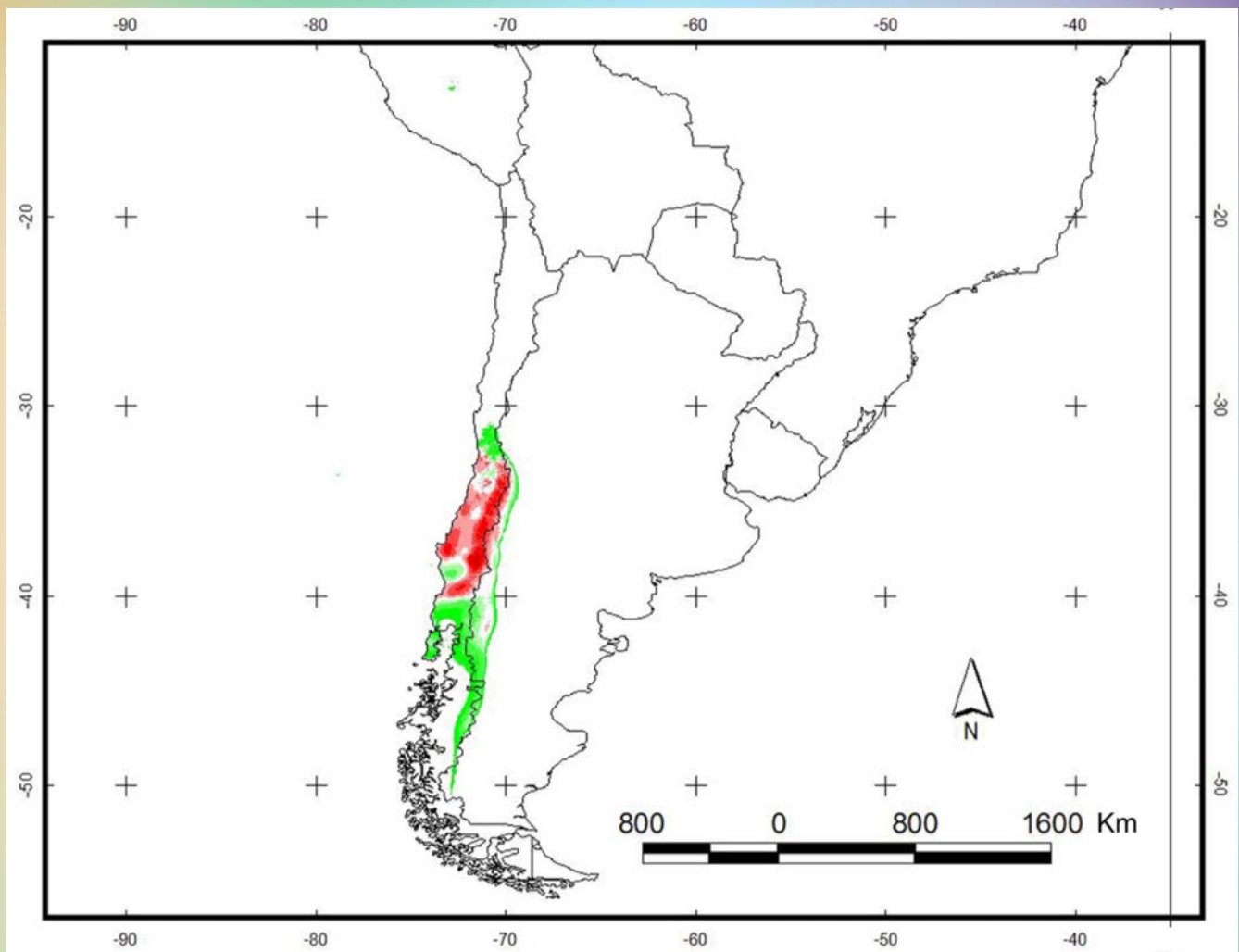


Fig. 1. Factores que determinan la presencia de una especie en un área geográfica determinada.

tos de recolecta de la especie en cuestión. Sin embargo, esta área puede estar ubicada, por ejemplo, en sitios donde se conoce históricamente que la especie no puede existir. Las razones que están involucradas tienen que ver directamente con los factores que delimitan el área de distribución de un taxón. Por ejemplo: en la figura 2 se muestra la predicción de un taxón, en este caso una especie de coleóptero de Chile central, *Eurymetopum modestum*. Este modelo de nicho ecológico fue elaborado a partir de 48 registros puntuales (Solervicens 1986, 2002) y 19 variables bioclimáticas (temperatura media anual, intervalo de temperatura media diurna, isoterma, estacionalidad de la temperatura, temperatura máxima del mes más caliente, temperatura mínima del mes más frío, intervalo de temperatura anual, temperatura media del trimestre más lluvioso, temperatura media del trimestre más seco, temperatura media del trimestre más cálido, temperatura media del trimestre más frío, precipitación anual, precipitación del mes más lluvioso, precipitación del mes más seco, estacionalidad de la precipitación, precipitación del trimestre más lluvioso, precipitación del trimestre más seco, precipitación del trimestre más caliente y precipitación del trimestre más frío; <http://www.worldclim.org/>) en Maxent, a una resolución de 0.01°. Es posible que este insecto no se encuentre pasando la Cordillera de los Andes en Argentina, ya que no se conoce de esas localidades, aunque el modelo de nicho ecológico predice que existen las condiciones ambientales para su supervivencia. Las razones para ello pueden ser variadas, desde que quizá se extinguió recientemente o no ha sido recolectado por falta de muestreo, hasta aquellas que



**Fig. 2.** Modelo de nicho ecológico de *Eurymetopum modestum* (Coleoptera: Cleridae) elaborado en Maxent a partir de 48 registros puntuales y 19 variables bioclimáticas. Los tonos en rojo indican mayor probabilidad de encontrar la especie, y disminuye conforme se torna verde.

predicen que en realidad se distribuye en ese sitio una especie muy relacionada con ella (especie hermana), o que los Andes han actuado como una barrera geográfica que ha confinado su distribución solo a Chile y por eso no se distribuye del otro lado de la cordillera.

Por los motivos antes señalados, se han generado diferentes métodos para proyectar un modelo de nicho ecológico como el área de distribución geográfica de un taxón, eliminando la sobrepredicción en los sitios donde se conoce que el taxón no puede estar o no ha sido registrado incluso con amplio esfuerzo de recolecta. Entre estos métodos podemos encontrar cinco básicos:

(1) Recorte (eliminación de la sobrepredicción) a partir de esquemas de regionalización previamente desarrollados, como ecorregiones o provincias bióticas (por ejemplo: Sánchez-Cordero et al. 2005). Este método sólo puede ser adecuado en dos casos, ambos para

evitar razonamientos tautológicos (circulares): si es que el resultado de la investigación no serán otros esquemas de regionalización y si las variables ambientales utilizadas en la generación del modelo no fueron incluidas para generar el esquema de ecorregiones.

(2) Recorte con coberturas que incluyan algún carácter histórico, tales como provincias fisiográficas (por ejemplo: Escalante et al. 2007), mapas geológicos, cuencas y subcuencas hidrográficas, terrenos tectonoestratigráficos, etc.

(3) Selección de las áreas en donde se tengan localidades conocidas, lo cual implica también considerar continuidad o discontinuidad de las áreas.

(4) Contrastación con mapas de distribución de la literatura (dibujados con otras metodologías, generalmente mapas "de manchas") y opinión de expertos (por ejemplo: Anciaes y Peterson 2006).

(5) Recorte con cartografía que represente alguna

interacción biótica en particular (por ejemplo, la distribución geográfica del huésped, de la especie polinizadora, etc.).

## Limitaciones y perspectivas

El uso de los modelos de nicho ecológico tiene muchas aplicaciones, sobretodo en la selección de prioridades de conservación en términos geográficos. Sin embargo, los modelos de nicho no deben utilizarse directamente como áreas de distribución, sino solo como aproximaciones a lo que pueden ser las áreas de distribución. Estos modelos resultan muy importantes para generar propuestas biogeográficas, pero creemos que su uso sin considerar sus implicaciones podría resultar, incluso, aventurado.

## Agradecimientos

Los datos de *Eurymetopum maculatum* fueron compilados por Francisca Neira y Miguel Rivas. Miguel Linaje y Gerardo Rodríguez colaboraron en el manejo del SIG y elaboración del modelo presentado en la figura 2. T. Escalante agradece la beca de PROFIP (DGAPA-UNAM) del periodo 2006-2007. P. Illoldi agradece la beca de posdoctorado al proyecto SEP-Conacyt 51562 durante el periodo 2007-2008.

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#### Patricia Illoldi-Rangel

Laboratorio de Sistemas de Información Geográfica, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Apdo. Postal 70-153, 04510 México, D. F., México; y Biodiversity and Biocultural Conservation Laboratory, Section of Integrative Biology, University of Texas at Austin, Austin, TX 78712, E.U.A.

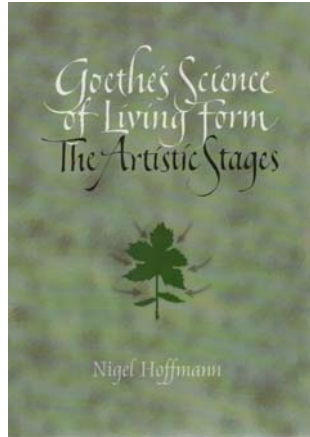
#### Tania Escalante

Museo de Zoología "Alfonso L. Herrera", Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Apdo. Postal 70-399, 04510 México, D. F., México.

## Goethe's science of living form: The artistic stages

BY MALTE EBACH

Goethe's science of living form: The artistic stages by Nigel Hoffmann. Adonis Press, Hillsdale NY, 2007, 173 pages, paperback, USD25.00, ISBN 0-932776-35-3.



It is rare to find a book that truly challenges the way we think about the world around us. Many texts would like us to think they challenge current ideas in science, however, few books would make us sit down, order a large cup of coffee and think "blimey". *Goethe's science of living form* is one such book. Modest in size (only 173 pages), Hoffmann has a lot to say and does so in a very well written and wonderfully illustrated volume.

The book starts off by going straight for the throat - questioning the validity of the hypothetico-deductive method, namely that a "... phenomenon is said to be explained when a casual relationship is proven" (p. 14). Hoffmann has put his finger on a very sore point in science, how to distinguish natural classifications from artificial systems, an issue explored by A.P. Candolle almost 200 years earlier. Hoffmann focuses on Candolle's contemporary, Johan Wolfgang von Goethe, the German poet, author and founder of comparative biology (although the latter is often forgotten or dismissed). Goethe coined the terms "comparative anatomy" and "morphology" and proposed a type of general homology that inspired a generation of comparative anatomists including A.P. de Candolle, Geoffroy Saint-Hilaire, Richard Owen and Adolf Naef. The central message of Goethe's work and Hoffmann's introduction is that we need to discover the *idea* rather than propose mechanical explanations.

In art as in science we study and describe form.

Our appreciation of form, the way it moves, grows and constantly changes, does not require reductionist mechanical explanations in order to make it more real or meaningful. A platypus does not need an explanation beyond itself. In having form, it can observe its relationship to other organisms. This however did not stop 19<sup>th</sup> century English anatomists from pulling a specimen apart to find out whether it was sown together, as if some meaning or explanation was to be found somewhere in a hemline. In treating organisms like machines that are made up of the sum of their parts we start to propose causes and generate explanations. "A machine", Hoffmann tells us, "is not an organism and is not free in any sense of the word; it is not free because it is entirely determined by something outside itself" (p. 13). This search for cause through mechanical explanation is what Hoffmann refers to as analytical thinking, something which scientists are trained to do. In order to see the world around us more clearly we need to dispense with this viewpoint. Hoffman continues:

"Remaining within its analytical mode of thinking, science will fail to grasp how the mechanical is taken up within the organic, how organic, creative laws hold sway and subsume the laws of cause and effect" (p. 19).

In effect, as practitioners of science and observers of the world, we are also actively part of the study of form, something that involves our own creativity, namely our ability to see and think. Hoffmann's message clearly follows on from Goethe, who proposed that intuitive perception could be a delicately empirical and objective way to observe and study form. Recently, Henri Bortoft and Ernst-Michael Kranich have also shown that descriptive science has a large intuitive component (not to be confused with "subjective"). Where Hoffmann's work stands out is in its application of a method to carry out descriptive science (i.e., taxonomy, systematics, biogeography, ecology). The first half of the book investigates these principles that stem partly from the work of Rudolf Steiner, while the second half is dedicated to the study of place.

Place is something in which biogeographers and ecologists specialise. While many ecologists confuse

population genetics with ecology, and biogeographers may confuse chorology with biogeography, place or landscape is central to all biogeographical and ecological studies. Hoffmann goes one step further, "...landscapes have a living organization - that is, an organization of organ-like structures..." (p. 77). The idea harks back to Humboldt's *Weltorganismus* to include the organic as well as the inorganic (i.e. Hegel's *geological organism*). Most important of all is that humans too are part of that same landscape and interact with it. Even as "objective" observers, it is impossible to step outside the world. Acknowledging that we interact with the landscape, reading what Hoffmann refers to as "the language of the landscape" (p. 93), can provide greater insight than normal analytical methods. The human, then, is an inverted landscape that can communicate that "language" as an idea through writing about it or through expressing it as art.

Hoffmann's work is no hocus-pocus-new-age-tree-hugging-hippie-crap. It is a genuine piece of scientific work that explores an area that we as analytical thinkers fear to tread – across the schism between the detached observer and the creative intellect. Many have tried to remedy this gaping fissure in human knowledge and fewer have succeeded. Hoffmann's work should be read with an open mind by the scientist who thinks that he or she knows better. I recommend this book to anyone interested in nature and who is actively engaged in taxonomy, systematics, biogeography or ecology.

**Malte C. Ebach**  
**International Institute for Species Exploration**  
**School of Life Sciences**  
**Arizona State University**  
**PO Box 876505**  
**Tempe, AZ 85287-6505**

# The Chinese Virtual Herbarium (CVH) and its future role for biogeographic research

BY LISONG WANG AND HAINING QIN

China is home to more than 31,000 species of vascular plants and more than half of them are found nowhere else (Yang et al. 2005). The species number of Chinese vascular plants species account for ca. 12% of the world known vascular flora (based on estimate of global vascular plants species of ca. 260,000; see discussion in Govaerts 2001, 2003; Scotland and Wortley 2003). These valuable inventory data are not only documented in national flora monographs, such as the *Flora Republicae Popularis Sinicae* (FRPS) (80 volumes and 126 books) and the ongoing *Flora of China* (FOC), but also in 34 local Chinese Floras that cover all most every province (Liu et al. 2007). Behind these Floras are the rich plant collections (ca. 16,135,547 specimens) preserved in over 300 registered Chinese herbaria. These rich biodiversity and biogeographic resources, however, are not easily accessible to the scientific community (Ma et al. 2007). To questions such as “how many species are there?”, “what are the biodiversity patterns in China?”, and “what are the conservation priorities at regional and local scales?”, scientists usually answer on the basis of fragmented, and frequently outdated, knowledge.

The Chinese Virtual Herbarium (CVH) project was therefore launched with the primary purpose to improve ability of scientists to answer these seemingly simple, but important, questions (Cracraft 2002).

## What is the CVH?

The Chinese Virtual Herbarium (Figure 1) (CVH: <http://www.cvh.org.ac>) is a part of ongoing biodiversity informatics project funded by the Ministry of Sciences and Technology of the People’s Republic of China (MOST) and the Chinese Academy of Sciences (CAS). During the past three years more than 30 herbaria and 110 botanists provided major contributions to the development of CVH. A network prototype is now online for the Catalogue of Chinese Vascular Plants (CCVP), the Occurrence of Chinese Vascular Plants (OCVP) and the Species and Specimens Gallery (SSG) (Figure 2).

The working team for this project is led by the Institute of Botany and the Chinese Academy of Sciences (IBCAS).

The CCVP data refers to published monographs and taxonomic revisions. Data quality is confirmed and controlled by more than 80 taxonomists. As shown in



Fig. 1. Web interface of the Chinese Virtual Herbarium.

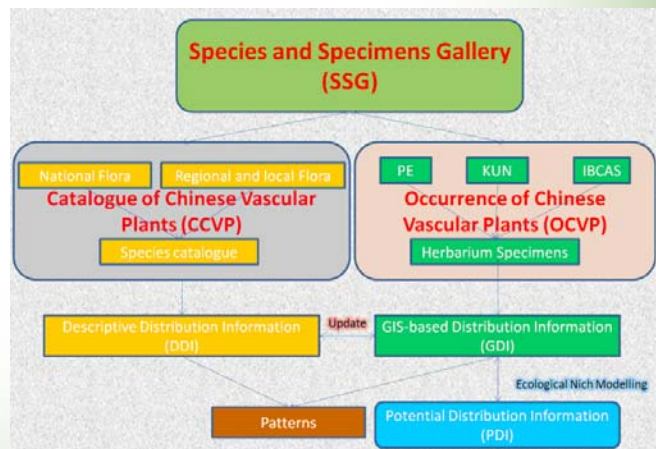


Fig. 2. The major data architecture in present CVH and its future biogeographic data flow chart.

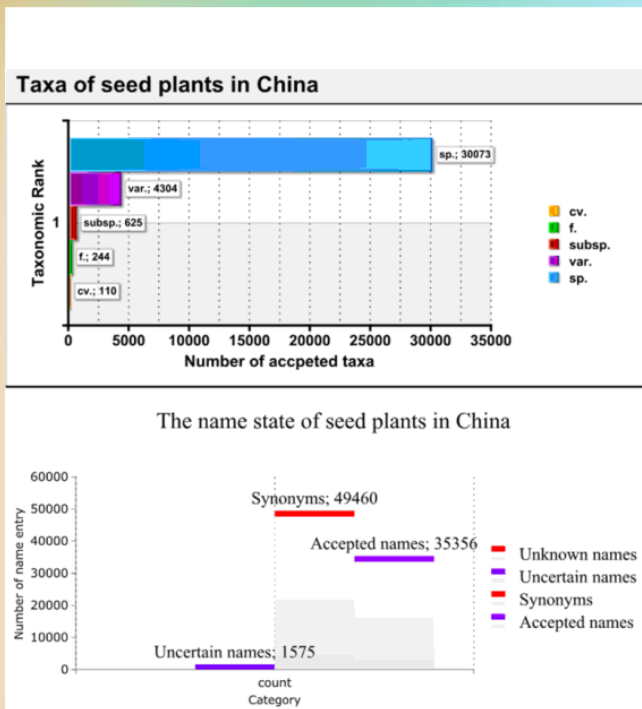


Fig. 3. Statistics of the incomplete Catalogue of Chinese Vascular Plants (CCVP).

Figure 3, the incomplete CCVP comprises 86,391 seed plant names (ferns are not displayed here) representing 49,460 synonyms and 35,356 valid names for 30073 species and 5283 infraspecies. With the exception of nomenclatural and bibliographic information, each named taxon includes detailed distribution information at the provincial, county to local level. Endemism at the provincial level is shown in Figure 4.

OCVP includes more than 2.7 million specimens and over 30 herbaria covering the major geographic, vegetational and biogeographical regions of China (Figure 5). Databasing for the Species and Specimen Gallery (SSG) has progressed rapidly over the last six months. It includes ca. 50,000 color field images for over 6,000 native Chinese vascular species. The large and heterogeneous sources for data require further work on the database design and web accessibility.

### How to build a strong link between CVH and biogeography?

The central mission of biogeography is to document and understand spatial patterns of biodiversity (Brown and Lomolino 1998). This simple definition obscures

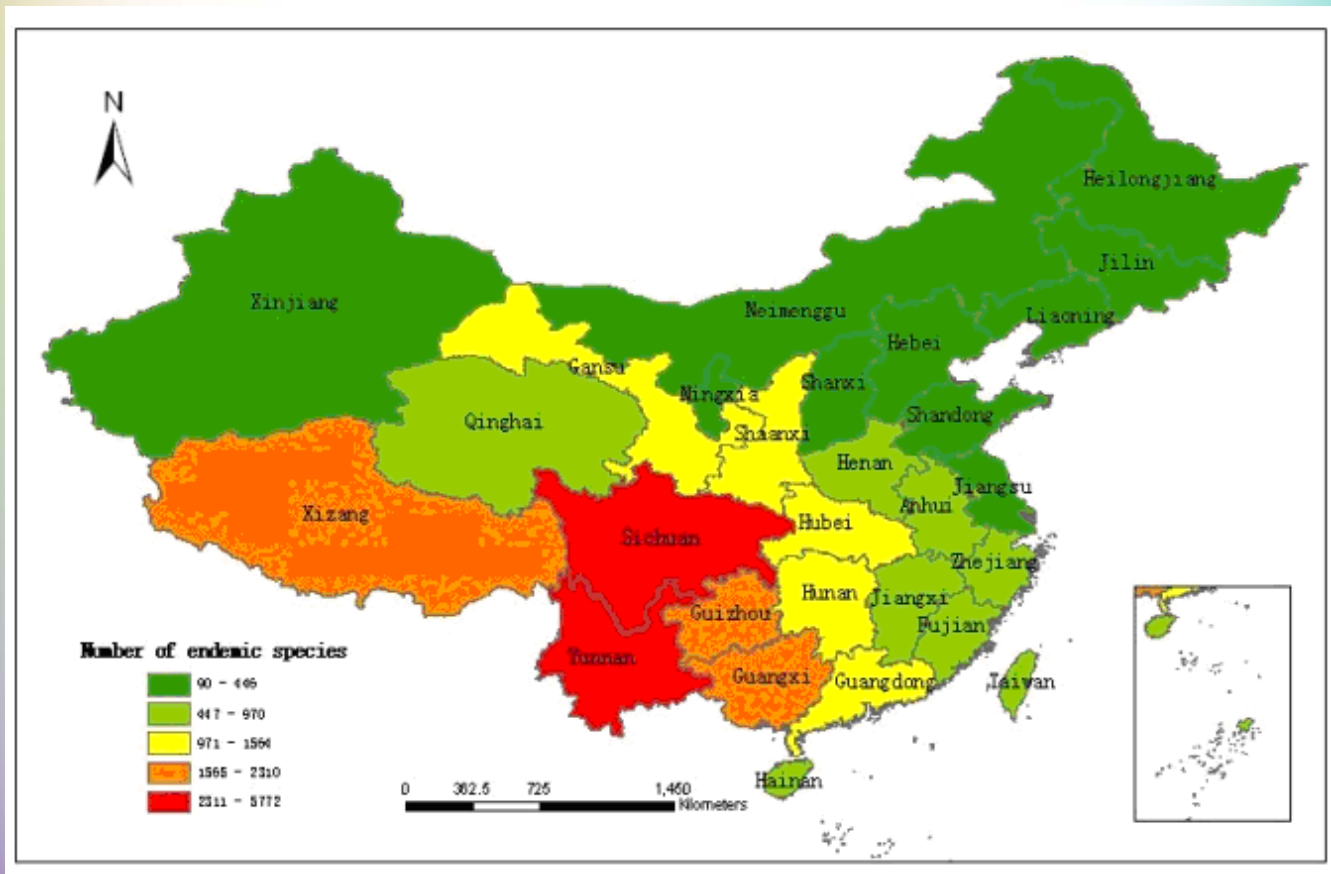


Fig. 4. Endemic species of China at provincial level.





**Fig. 5.** Geographic placement of herbaria participating in the CVH.

the complexity of the discipline (Crisci 2001; Posadas et al. 2006), and the many discussions about its theoretical foundations (Hovenkamp 1997; Morrone 2001, 2002, 2005; Ebach and Humphries 2002, 2003; Ebach & Morrone 2005), research traditions, and methods (Myers and Giller 1988; Morrone and Crisci 1995; Brown and Lomolino 1998; Cox and Moore 2000; Crisci 2001; Crisci et al. 2003, 2006; Ferguson 2004; Van Veller 2004).

Irrespective of research traditions (historical vs. ecological) (Posadas et al. 2006) or methods, the acquisition of distribution data is first and foremost – whether from inventory lists or from herbarium specimens. The two data sources have generally been used in the investigation of species richness or patterns of endemism for a target area or taxon (Crisp 2001; Crisp et al. 2001; Linder 2001; Laffan and Crisp 2003; Barthlott et al. 2005; Kier et al. 2005; Linder et al. 2005; Mutke and Barthlott 2005; Galley and Linder 2006; Heads 2006; Qian et al. 2006, 2007; Zhao and Fang 2006; Zhao et al. 2006; Born et al. 2007; Klopper et al. 2007; Qian 2007). In response to these biogeographic requirements we established CCVP and OCVP to produce Descriptive Distribution Information (DDI) and GIS-based Distribution Information (GDI), respectively (Figure 2).

DDI is used to indicate that the distribution information has usually been recorded with respect to an administrative boundary (such as at province or county), with the range presented as text or coarse range map. The use of DDI to identify floristic elements (Hausdorf 2002; Hausdorf and Hennig 2003), distribution patterns, and floristic realms or regions is a common practice in biogeography (Mayr 1944; Thorne 1972, 2004; Good 1974; Takhtajan 1986; Wu 1991, 1996; Cox 2001; Cox et al. 2002; Wu et al. 2006; Finnie et al. 2007; Moreira-Muñoz 2007). Biogeographic models and hypotheses are derived from this classical research practice, include

the land bridge theory (Van Steenis 1962), the Eastern Asia-Eastern North American (EAEN) disjunction model (Li 1952; Wu 1983; Wen 1999; Qian 2001; Wen 2001; Xiang et al. 2004; Nie et al. 2006), the East Asia realm (Wu 1996), and the floristic delimitation of Chinese seed plants (Wu and Wang 1983; Wu 1991) (Figure 6). But DDI data are not easily exchangeable for use in comparative biogeographic analysis (Noonan 1999). We will provide a web service for transformation of administrative-based distribution data into biogeographic units such as ecoregions, floristic realms, provinces and regions.

The application of DDI in biogeography is, however, deficient because it usually relies on heuristic techniques of classification based on visual inspection and expert opinion (Finnie et al. 2007). The resulting biogeographic models usually give more emphasis to shared similarities than differences. For example, there are more than 120 angiosperm genera classified as EAEN (Wu 1983) that may differ in distribution details such as their centers of distribution or disjunction distance. Attempts to provide an integrated interpretation of distributional relationships based on a coarse range map may, therefore, overlook pertinent information. As noted by Brown and Lomolino (Brown and Lomolino 1998), ‘Even the best map, however, can convey only a highly simplified and abstracted picture of the geographic distribution of a species. The real units of distribution are the location of all the individuals of the species’.

The application of GIS and related techniques may provide the means by which to achieve the biogeographer’s goal by drawing upon all individual records of each species on a single map layer. The benefits of GIS-based species distribution maps in biogeography are demonstrated in many studies (Noonan 1999; Hijmans and Spooone 2001; Bletter et al. 2004; Chapman 2005; Miller and Knouft 2006; Stigall and Lieberman 2006; Hijmans et al. 2007), including floral atlases (Finnie et al. 2007), quantified analyses of species richness and endemism (Crisp et al. 2001) and ecological niche modelling (Yesson and Culham 2007). We regard DDI and GDI as complementary approaches that address different goals but the combination of DDI and GDI is necessary to build a biodiversity map based on reliable and verifiable sources and quantitative analyses. This map will provide an informative beginning for a broad range of biogeographic studies at the regional and local scale, as a starting point to investigate all kinds of biogeographic phenomena at regional and local scale.

## Perspectives

During the last decades biodiversity informatics projects sharing digitized inventory lists and herbarium

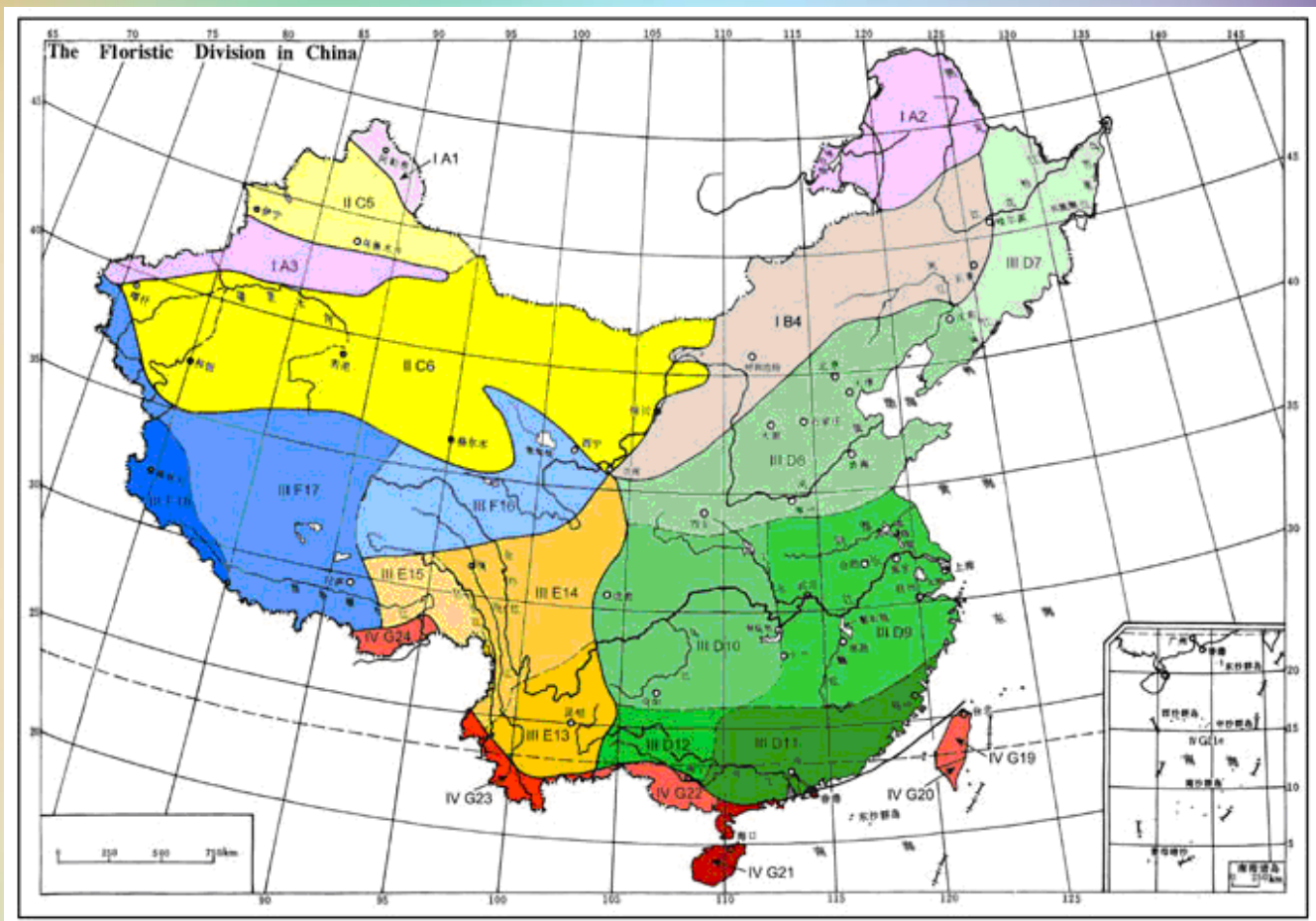


Fig. 6. Floristic divisions in China (published by C. Y. Wu 1991, illustrated by Yaodong Qi).

specimens have developed on the internet. Their data coverage ranges from the global and regional local scale. The GBIF has played a leading role by sharing over 120 million biological collections records. However, as reported by Yesson(2007), its data quality and spatial coverage is deficient. This situation is not uncommon for biodiversity informatics projects involving large geographic units, many biological groups, and large databases.

Biogeographic patterns such as species richness and endemism are, however, strongly linked with the specified spatial scale (Crisp et al. 2001; Whittaker et al. 2001; Laffan and Crisp 2003) so a hierarchical research scheme connecting global with local, and macro-to-micro scale is necessary for both biogeography (Whittaker et al. 2001), and the construction of a biodiversity information network.

As mentioned above, when facing diverse user requirements, rapid scientific and technological progress is much more flexible and easy to control for small databases. We can imagine a global biodiversity information network as a pyramid bolstered by many small, flexible, high quality databases. In this sense, CVH will

play a central role for future biogeographic studies of global and regional biodiversity.

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**Lisong Wang and Haining Qin**

**Institute of Botany, Chinese Academy of Sciences,  
100093 Beijing, China.**

**lswang@ibcas.ac.cn**

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