

Biocomplexity and conservation of biodiversity hotspots: three case studies from the Americas

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The perspective of 'biocomplexity' in the form of 'coupled natural and human systems' represents a resource for the future conservation of biodiversity hotspots in three direct ways: (i) modelling the impact on biodiversity of private land-use decisions and public land-use policies, (ii) indicating how the biocultural history of a biodiversity hotspot may be a resource for its future conservation, and (iii) identifying and deploying the nodes of both the material and psycho-spiritual connectivity between human and natural systems in service to conservation goals. Three biocomplexity case studies of areas notable for their biodiversity, selected for their variability along a latitudinal climate gradient and a human-impact gradient, are developed: the Big Thicket in southeast Texas, the Upper Botanamo River Basin in eastern Venezuela, and the Cape Horn Archipelago at the austral tip of Chile. More deeply, the biocomplexity perspective reveals alternative ways of understanding biodiversity itself, because it directs attention to the human concepts through which biodiversity is perceived and understood. The very meaning of biodiversity is contestable and varies according to the cognitive lenses through which it is perceived.

Keywords: biocomplexity; biodiversity; connectivity; hotspots

1. INTRODUCTION: BIODIVERSITY, BIOCOMPLEXITY AND CONNECTIVITY

Biodiversity is often conceived to exist independently of human social and cultural systems, which are often conceived per se to threaten it (Noss & Cooperrider 1990). This way of thinking is especially tempting in the context of the Americas, which were believed to be in a hemisphere-wide wilderness condition prior to 'discovery' by Europeans only half a millennium before the present (Nash 1967). The wilderness myth has now been debunked and the conservation strategies in the Americas that were implicitly based on it are both incomplete and problematic to the extent that they ignore past and present interactions of human and natural systems (Callicott & Nelson 1999). The more recent emergence of the concepts of biocomplexity and connectivity provide a way of re-integrating present and future human systems into conservation strategies. Further, when the concept of biocomplexity is overlain on the concept of biodiversity, the latter may prove to be more multi-faceted than once it seemed. We begin with a brief overview of the concepts of biodiversity,

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biocomplexity and connectivity. We indicate that biodiversity is an evolving concept that proves to be ambiguous when expressed precisely and quantitatively. We also provide an account of the less familiar concept of biocomplexity and its relationship to the evolving science of complex systems. And finally, we indicate the special sense in which we employ the concept of connectivity.

(a) Biodiversity

The term 'biodiversity' came into common usage in the conservation community after the 1986 National Forum on BioDiversity held in Washington, DC and the publication of selected papers from that event, titled Biodiversity, edited by Wilson (1988). Wilson (1988) credits Walter G. Rosen for coining the term. However, the *concept* was ambient in ecology, since at least the mid-twentieth century, under the simpler rubric of 'diversity', and was implicitly understood to mean the species richness of a biotic community. Diversity was often causally coupled with the illdefined concept of 'stability'. Transforming it from an ecological shibboleth to something more precise, MacArthur (1955) expressed the 'diversity-stability hypothesis' quantitatively, controversially borrowing the Shannon-Weaver index from information theory as a metric (Shannon & Weaver 1949). To richness, use of

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the Shannon-Weaver index added evenness of abundance distribution of the species present in a biotic community to the concept of species diversity. Belief in the positive correlation between species diversity and ecological stability began to erode in the last quarter of the twentieth century, but has been revived at the beginning of the twenty-first century (Goodman 1975; Chapin et al. 2000; Lehman & Tilman 2000; McCann 2000). Whatever the eventual outcome of that ongoing debate, alarm at the magnitude of global anthropogenic species extinction in the 1980s decoupled concern for the loss of biodiversity with concern for ecosystem stability. Many other rationales for species preservation have since been advanced (Wilson 1992). In addition to species richness and evenness of abundance distribution, biodiversity is also latterly understood to comprise genetic and population diversity within species and diversity among biotic communities, ecosystems and their internal structures and processes (Noss 1990; Groom et al. 2006).

We provide these brief remarks about the concept of biodiversity to indicate how an idea that seems plain enough on its surface proves to be very elusive when one attempts to specify, quantify and measure it. For example, the Shannon-Weaver index associates biodiversity with thermodynamic entropy, as MacArthur (1955) himself expressly noted. Later, however, Odum (1969) correlated increased biodiversity with increased ecosystem organization and opposed it to entropy. Moreover, the evenness parameter of the Shannon-Weaver index has little correspondence to bioticcommunity trophic structure—because numbers of individuals at higher trophic levels must be fewer by orders of magnitude than those at lower levels (Elton 1927; Lindeman 1942). Nonetheless, the Shannon-Weaver index remains useful when applied to guilds (Nai-Bregaglio et al. 2002; Kunst et al. 2003).

Further, Sarkar (2002) observes that it is impossible to count all the species of a biotic community or landscape at scales relevant to conservation, let alone the numbers of individuals representing each species present, and therefore that conservation biologists must select 'surrogate' species to represent an area's total biodiversity. The necessity of selecting surrogates, however, may lead to under appreciating the biodiversity of areas where the usual surrogate species may be poorly represented (Rozzi et al. 2003a). For example, Myers et al. (2000) identify hotspots for conservation priority using vascular plants as surrogates. Here, we suggest using alternative taxonomic groups—such as bryophytes—as surrogates for or indicators of biodiversity in a region of high latitude where vascular-plant diversity is limited. In addition to the methodologically imposed ambiguities of the concept of biodiversity, effective conservation strategies might profitably take into account the past and present human systems with which biodiversity coexists. In other words, effective conservation strategies might well consider biocomplexity as well as biodiversity.

(b) Biocomplexity

The wilderness myth has obscured the extensive impact of human habitation and exploitation of north-, central- and south-American biomes throughout the Holocene (Denevan 1992; Gomez-Pompa & Kaus 1992). Natural

and human systems in the Western Hemisphere have been coupled in complex, dynamic interactions for at least 11 000 years. Notoriously, the arrival of *Homo sapiens* in the Americas was followed by a spasm of megafaunal extinctions and the aetiological link between the two events has been the subject of on-going debate (Barnosky *et al.* 2004). Subsequent cultural adaptation to a wide range of reorganized ecosystems in the Americas was equally varied—and has also been the subject of on-going debate.

For example, Gomez-Pompa & Kaus (1990) argue that supposedly natural Central American rainforests were systematically and sustainably managed by the Maya and other indigenous peoples. On the other hand, Brenner et al. (2001) argue that, by the ninth century CE, Mayan swidden horticulture caused extensive deforestation, soil erosion and nutrient depletion. Exacerbated by a drier climate cycle, war and political instability, Mayan ecological mismanagement precipitated a social and a demographic collapse. Both these apparently contradictory stories about the complex, dynamic interaction of Mayan culture and society with the natural systems of Central America could be true. The Maya settled the region about the time Homer was composing the Iliad and over two millennia the way they interacted with the ecosystem they inhabited surely changed. In addition to temporal variability, Maya land use surely also varied spatially, such that the sustainable agroforestry practices that Gomez-Pompa & Kaus (1990, 1992) infer from the current composition of Central American rainforests might have existed contemporaneously with the less sustainable swidden practices that Brenner et al. (2001) infer from the sedimentation rates of lakes and the pollen record.

In addition to the work of Brenner and his associates and that of Gomez-Pompa & Kaus, the mutual interactions of humans with their natural environments have been the subject of systematic study for many years (Turner 1976; Turner et al. 1990; Redman 1992, 1999; Kasperson et al. 1995; Gragson 1998; Evans & Morán 2002). Just as the concept of biodiversity existed before the term was coined, the term 'biocomplexity' was coined at the beginning of the twenty-first century to characterize, among other phenomena, multiple levels of biological organization, interacting feedbacks and the nonlinear emergent behaviour of coupled natural and human systems (CNHS) as they evolve through time (Covich 2000; Dybas 2001; Cottingham 2002; Pickett et al. 2005). While studies of the mutual interactions of humans with their natural environments are not new, the development of new mathematical techniques has increased our capacity to understand them.

It is almost trite to observe that natural and human systems interact in complex ways—when the term 'complex' is used in the colloquial sense. However, a deeper understanding of the dynamics of interacting systems has developed recently within the field of complex systems science (Ablowitz & Athanassios 2003). Within this more technical context, complex systems are characterized by inherent limitations in the ability to predict long-term or emergent behaviours. The limits of predictability arise from the nature of the nonlinear interactions between system components

and from the impossibility of measuring the state of the system—the initial conditions—at any time with precision (Adami 2002; Burggren & Monticino 2005). Thus, traditional analytical methods were inadequate to study complex systems. More sophisticated methods of analysing dynamic systems and modelling simulation techniques, such as cellular-automata and multi-agentbased models, and increased computational capacity now allow us more comprehensively to understand the dynamics of complex systems, such as CNHS.

In particular, it is now possible to simulate the complex dynamics of natural succession as well as urban, suburban and exurban development or clearing, planting or pasturing in forested landscapes (Acevedo et al. 2001, 2005; Deadman et al. 2004; Monticino et al. 2004, 2005; Quintero et al. 2004). These methods may be more generally enlisted in the cause of biodiversity conservation. By simulating the dynamics of complex natural systems that harbour biodiversity and that are also coupled to complex human systems which threaten it, individual stakeholders and policy makers may anticipate a suite of emergent patterns before any actually evolve in real time. Thus, individual actions and public policies may be chosen to try to optimize the values of biodiversity conservation and economic development. In addition, the study of CNHS-type biocomplexity may reveal historic synergies and symbioses between human systems (human life ways and livelihoods) and natural systems that may be useful for future biodiversity conservation strategies.

(c) Connectivity

We use the term 'connectivity' to refer to the interface between CNHS (Acevedo et al. in press). In general, human systems are connected to natural systems in two basic ways-materially and psycho-spiritually. In CNHS, stakeholders derive a portion of their food, fodder, water, building sites and materials, medicines and other natural resources and ecosystem services from the local environment; and in some this material connectivity is stronger than in others. In CNHS, stakeholders also derive a portion of their religiously significant sites, aesthetic experience, and personal, cultural, and/or ethnic identity from the local environment. This mode of connectivity also varies in strength. Biodiversity may be critically important to both these modes of connectivity. As to the former, the current and option value of biodiversity for such things as new foodstuffs and medicines is too familiar to warrant rehearsing here (Wilson 1992). The case for the aesthetic and even spiritual value of biodiversity is almost as familiar as the case for its material value (Kellert & Wilson 1993). While material connectivity varies significantly among various CNHS in degree, it varies less significantly between them in kind. Psychospiritual connectivity, however, varies significantly among sites not only in degree, but also in kind. To illustrate, while maize, for example, is a foodstuff grown both in North and South America and, in both places, trees are harvested for building materials and fuel wood and cattle are pastured in grasslands, the cultural significance and even perception of biodiversity may vary more radically from place to place.

In the three case studies that follow, we identify the respective nodes of connectivity that could be important to the future conservation of biodiversity in each. They are examples of temperate coastal, inland tropical and maritime sub-polar forest landscapes, respectively. In addition to the representative points on the global latitudinal climate gradient, we focus our discussion on these areas because they also lie on a gradient of human impact on natural systems. All three areas are partly protected. The Big Thicket National Preserve (BTNP) is a fragmented group of small conservation units in a rapidly urbanizing rural matrix. The much larger Cape Horn Biosphere Reserve is located in one of the most remote and least populated regions of the world. The Upper Botanamo River Basin (UBRB), at the edge of the large Imataca Forest Reserve (IFR), falls between these extremes of high and low impact of human systems on natural systems; it is subject to pressures analogous to those of the Big Thicket (BT), but so far, they are less intense and less widely distributed.

For each of these areas, we provide a condensed biocultural history as background. We suggest that a consideration of the cultural aspect of that history—in its broadest sense, the history of specific human interactions with specific biota—as well as the biological aspect provides an important dimension of understanding for biodiversity preservation in the future. The indigenous cultural traditions of the BT are largely lost, but have been supplanted by an Anglo-American romance of recent provenance. In part owing to the prominent role they play in Darwin's Voyage of the Beagle and The Descent of Man, the Cape Horn region, by contrast, is as famous for its indigenous peoples and their aboriginal culture as for its treacherous waters, rugged mountains and fierce winds. In the UBRB, indigenous peoples and their cultures remain robust, but they increasingly face competition from a more cosmopolitan urban, agricultural and industrial cultural complex.

In §5 that follows the three case studies, we compare the opportunities for biodiversity conservation afforded by a consideration of the cultural history and material and psycho-spiritual connectivity in each of the hotspots we review. More philosophically, we indicate how the biocomplexity perspective reveals alternative ways of conceptualizing biodiversity, because it directs attention to the human cognitive framework through which biodiversity is perceived and understood. We demonstrate how the meaning of biodiversity is variable and may shift in surprising ways when the cognitive lens through which it is first perceived is exchanged for another.

2. THE BIG THICKET

The BT is an ill-defined region of southeast Texas on the coastal plain of the Gulf of Mexico lying north of the city of Beaumont at approximately 30° N/94° W. Early estimates of its aboriginal size vary from 10 to 15 000 km² (Parks 1938; McCleod 1972). Its current size is regarded to be approximately 2100 km² (Marks & Harcombe 1981; Harcombe et al. 1993). It receives annual rainfall of 1341 mm, evenly distributed throughout the year; average annual temperature is approximately 10°C, with an average of 240 consecutive frost-free days per year (National Climate Data Centre 1994). The BT is home to more than 100 tree and shrub species, more than 1000 herbaceous plants—including 26 ferns, 20 orchids and four of five species of North American insectivorous plants—and some 50 kinds of reptiles; more than 300 species of birds reside in or migrate through the area (Parks & Cory 1932; National Park Service 2005).

The predominant flora and fauna of the BT are characteristic of the warm, humid North American forests that stretch from east Texas to South Carolina (Harcombe et al. 1993). Because such forests have extensively been logged and/or converted to other uses, any representative remnant is a worthy candidate for preservation. Topographic and edaphic conditions in the BT have powerfully influenced the local segregation of this rich concentration of plant species into distinctive plant communities—adding community- and landscapelevel to species diversity. The longleaf-pine (Pinus palustris) plant formation was once dominant, but is now among the most threatened in North America (Marks & Harcombe 1981). It is fire-dependent, and so, with fire suppression, has disappeared from well-drained landforms in the BT, having been replaced by mixed forests of loblolly pines (Pinus taeda) and oak hardwoods (Quercus nigra, Q. hemisphaerica, Q. alba, Q. falcata, Q. stellata), which were once more restricted in extent. In BT uplands and some stream bottoms with sandy-loam soils that are well drained, but moist throughout the year, magnificent stands of southern magnolias (Magnolia grandiflora) and American beech (Fagus grandifolia) are dominant. Sloughs and oxbows of river and creek floodplains are dominated by baldcypress (Taxodium distichum) and tupelo (Nyssa aquatica) swamps; floodplains along creek and river corridors contain bottomland-hardwood forests of oaks (Q. nigra, Q. lyrata, Q. michauxii and others) and gums (Liquidambar styraciflua, Nyssa sylvatica) (Marks & Harcombe 1981).

The BT was less attractive to indigenous agriculturists than the better-drained and richer soils of the uplands and river floodplains to the north (Cozine 2004). High rainfall, coupled with poor drainage characteristic of low, flat terrain resulted in extensive growth of wetland brush bogs—dense stands of mostly evergreen shrubs, now locally called 'baygalls'—that made human travel through the region difficult (Gunter 1971). Doubtless it was these plant associations that gave the place its name. Thus, the BT remained in a condition of low human impact throughout most of the Holocene, neither inhabited nor oft frequented by American Indians. After the settlement of the surrounding region of Texas by European- and African-Americans, the BT stayed largely uninhabited by humans (Cozine 2004). Before the American Civil War it was a refuge for runaway slaves, during that war it was a haven for draft dodgers and conscientious objectors, and thereafter it was a hiding place for outlaws and other social renegades (Cozine 2004).

Exploitation of the rich timber resources of the BT began in earnest during the last quarter of the nineteenth century; at about the same time, oil was discovered in the region, leading to a drilling boom (Cozine 2004). During the first quarter of the twentieth century, much of the land was acquired by big timber companies, and the forests began to be rapidly reduced,

especially the long-leaf pine. As early as the 1930s, concerted efforts to preserve a remnant of the BT began (Gunter 1997). After a bitterly fought political struggle pitting the state and federal governments against each other, as well as the economic interests of the timber barons against the concerns of conservationists, the BTNP was created under the auspices of the US National Park Service in 1974, currently consisting of nearly 40 000 ha, in 15 discrete units, connected by riparian corridors (Cozine 2004; National Park Service 2005). This was the first property added to the American national park system owing to its biodiversity—a decade before the term would be coined. For the same reason, the BTNP was added to the United Nations International Biosphere Reserve system in 1981 (National Park Service 2005). Of the aboriginal BT, only approximately 2-5% is legally protected—and in highly fragmented parcels. In the 1990s, the timber companies, which were the largest private landowners in the region, began to sell off their holdings. Formerly, the matrix between conservation units, while not protected, had at least remained in one or another stage of forest succession. Now that matrix is subject to land-use/land-cover (LU/LC) changes associated with urbanization that are more irreversible than timber harvesting.

In most of the United States, human material connectivity to local natural systems has declined with time—and the BT is no exception. The sparse agriculturists of the early twentieth century in the region locally produced much of their foodstuffs and livestock feed, and locally harvested wildlife, building materials and fuel wood; but as time went on, like most Americans, denizens of the BT increasingly relied on the global market for material sustenance. Psycho-spiritual connectivity to the BT was based in large part on its romantic past as untrammelled 'wilderness,' enlivened by big fierce wild animals (including charismatic megafauna such as black bears, red wolves, alligators, panthers and feral hogs) and leavened by fiercely defiant feral men (outlaws, draft dodgers and renegades).

In addition, part of the psycho-spiritual connectivity to the BT is its reputation as the 'biological crossroads of North America'—as it were, a four-surfaced ecotone and an 'American ark' (Bonney 1969; Bloomfield 1972; Gunter 1993). The region is supposed to have been a Pleistocene floristic refugium, where one finds relict plant communities now more characteristic of (i) the deserts of the Southwest, (ii) the prairies of the Central Plains, (iii) the forests of the Ohio and Tennessee river valleys and (iv) the swamps of the Southeast (National Park Service 2005). Also found are the fauna that typically inhabit such communities. Other scientists, however, dispute this characterization (Marks & Harcombe 1981). This discrepancy may be a function of the cognitive lens through which the BT is perceived. Through a temporally thick, climatological and evolutionary lens, the region is a nexus in the ebb and flow, mix and match of temporally and spatially dynamic species. Seen through a temporally thin, ecological cognitive lens, the region's climate is regarded as relatively stable during the Holocene and the species diversity of its biotic communities appears to be typical of the coastal plain eastward to Georgia and Florida, its

dramatic community- and landscape-level diversity being attributable to locally abrupt edaphic and topographic gradients.

Contemporary residents of the BT express complex and often contradictory attitudes towards and values concerning the land and biota. These attitudes and values may derive from the unique mix of outlaw spirit, romance with wild places and dreams of quick wealth that imbues so much of the Texas experience. As part of a LU/LC change study, we conducted a survey of owners of large tracts (greater than 100 acre) of undeveloped land in a subsample of the BT region. The overall objective of the survey was to elicit circumstances and values that lead to LU/LC changes in the region. In particular, a portion of the survey focused on what factors influence noncommercial landowners to sell their land for eventual high-density residential or commercial development. While the absolute number of survey respondents was not large, the responses represent 30% of the individuals owning large parcels in the region. The responses validate anecdotal accounts of regional attitudes obtained through separate interviews with local conservation activists and real estate agents (Gunter 1997).

BT landowners use their property for a variety of things—primary residences, second homes, hunting, timber harvesting, cattle ranching and investment property. Their LU attitudes and values separate them into two broad groups: (i) those who express a deeper attachment to land that they themselves have lived on for a long time or that has been in their family for generations and (ii) those who value land primarily for its economic potential. The latter typically either acquired their lands for timber harvesting, or bought in recently, speculating that the properties would increase in value for profitable resell. The former tend to be older, having bought or inherited land decades ago. Those who inherited their properties often express the hope of keeping them in the family. For instance, a common statement from this group was that the land is 'part of my heritage since way before the turn of the century...a homestead for future generations...meant to be in the family'. Many of these landowners also express genuine concern about preserving open spaces, wildlife habitat and landscape integrity. And yet, the same people that would 'love for (the) area to stay as is, with trees' also welcome the convenience of the new roads and stores attending residential development. This contradictory view appears to arise from two psychological postures: resignation to perceived progress and pragmatism when faced with less desirable alternatives. Expressions such as 'city people in rural areas are just part of life' illustrate resignation. A greater preference for commercial and residential development 'than trailers sitting around (the) beautiful (Big) Thicket' illustrates pragmatism. In addition, many express a strong Lockean belief that landowners should be able to do what they want with their property, free from 'lots of government restrictions'.

Given these conflicted attitudes—appreciating the natural surroundings but not hostile to developmentthe trend of ever-expanding suburban sprawl extending from the Houston-Beaumont area is likely to continue unless governmental and non-governmental

conservation organizations get aggressively involved in the recently expanded BT real estate market. Otherwise, development right up to the borders of the BTNP is likely, mitigated here and there by undeveloped parcels held by tenacious long-time residents and tradition-valuing families.

The biocultural history of the region might be deployed to encourage forms of development supporting biodiversity conservation, complementing efforts to acquire and sequester additional lands. The popular evolutionary romance of the BT—as a biological crossroads and ark—is historically linked to its historical romance. The earliest effort to conserve a sizeable remnant of the BT was motivated by a concern for disappearing 'game' species, especially deer and bear, and the kind of men who hunted them (Gunter 1997). From the 1930s onward, the conservation impulse matured and eventually manifested itself as a concern for biodiversity. The combination of low material connectivity and high psycho-spiritual connectivity of the CNHS in the BT suggests an additional strategy for the conservation of its biodiversity. New residents to the region extract few of their material resources from the landscape, except home sites and transportation and commercial infrastructure. The BT therefore could be developed in such a way-e.g. high-density residential clusters-designed to preserve a significant degree of the historic forested character of the region.

3. THE UPPER BOTANAMO RIVER BASIN

The UBRB is located in the southeastern section of the Guiana Shield of Venezuela, which is a very sensitive hydrological and biogeographical region of South America (Rosales 2003; Rosales et al. 2003). The UBRB occupies 2556 km², and about half of this surface is within a protected area, the IFR. Mean annual air temperature is 26°C, exhibiting little variability. Rainfall is seasonal with bimodal distribution and an annual mean of 1284 mm (UCV-MARNR 2002). Associated with a spatial precipitation gradient, there are, respectively from high to low, evergreen forests, semi-deciduous forests (i.e. a mix of evergreen and deciduous species), and scattered savannahs within the latter (CVG TECMIN 1987). The canopy height of the evergreen forests typically exceeds 25 m and includes high plant diversity. The UBRB is mostly a peneplain relieved by low hills. Towards the northeast sector (Serranía de Nuria), one finds much higher hills.

Complex human and biophysical interactions generate LU/LC changes in the UBRB protected areas to the west as well as in those that are unprotected (Delgado et al. 2005). These changes may be indicative of future changes in the structure, composition and biodiversity of the rest of the IFR, which is considered to be one of the most valuable forest reserves in Venezuela and South America, characterized not only by the abundance of commercially valuable timber species and genetic wealth, but also by the overall species richness and a variety of fragile ecosystems (Miranda et al. 1998; UCV-MARNR 2002). The IFR is also home to five indigenous ethnic groups, whose livelihoods and cultures depend on their natural surroundings: the Warao, Arawako, Kariña, Akawaio and Pemón Indians (Mansutti et al. 2000).

The UBRB and the IFR are part of the East Guayana biological province. Like the BT, the region is something of a biological crossroads. It contains lowland neotropical flora, as well as vegetation characteristic of the Guiana Shield. It is a centre of speciation in its own right, having evolved a welldefined biota, but species that evolved in adjacent speciation centres, especially the Andes and the Amazon, are also found there (Berry et al. 1995). The vegetation in the IFR varies dramatically—from seasonally flooded evergreen forests dominated by Mora gonggrijpii and Mora excelsa to Trachypogon savannahs dominated by herbaceous plants (Berry et al. 1995). The region is home to more than 2000 vascular-plant species: 368 species (palms, flooded forests and grasslands) are associated with areas of poor drainage; 1260 species compose the evergreen forests and intermediate savannahs; 589 species compose slope forests, shrub lands and the vegetation of tepuy (tabletop) mountain summits; 197 species compose deciduous and semi-deciduous forests; and 376 species compose the forests of the Nuria high plateau (UCV-MARNR 2002). The region is also home to a significant number of endangered species (Hernández et al. 1997; Llamozas et al. 2003).

The vegetation cover within the UBRB varies greatly in response to variations in land use. In the northwest sector, where the semi-deciduous forests were historically predominant, the creation of pastures has effectively shifted the land cover from forest to savannah. Human disturbance in this part of the UBRB is so great that herbaceous vegetation is now predominant. Extensive riparian or gallery forests and forested fragments of various sizes, however, have survived. Secondary vegetation in different stages of succession is also present in abandoned pastures. In the zone of urban expansion around Tumeremo, the main population centre, and along the routes of penetration into the forests, the forests have been exposed to strong pressure from subsistence agriculturists. This has created a mosaic of various land covers: conucos (plots of cultivated land), grazed savannah, forest fragments and grasslands. In response, the abundance and diversity of plant and animal species is changing (Delgado et al. 2006). However, in the eastern part of the UBRB, there remains a large expanse of humid tropical forest, which is almost completely located within the IFR. Here, the forests have undergone changes in composition and structure, but the continuity of the canopy has remained fairly stable. Habitat loss and forest fragmentation constitute major threats to biodiversity in the UBRB and should be the targets of control in management and conservation strategies.

The main LU changes within the UBRB can be summarized in four historical phases (Carrocera 1979). (i) Until the mid-seventeenth century, it was populated only by the Kamaracoto indigenous groups, who practised swidden agriculture, as the indigenous people still do in the continuous forests of the UBRB. (ii) In 1788, the Spanish founded a mission at Tumeremo, a site selected owing to favourable conditions for cattle ranching, thus initiating the process of forest

fragmentation. By the nineteenth century cattle ranching encircled public lands around Tumeremo in a 5 km radius. (iii) Latex began to be extracted and gold mined in the first half of the twentieth century. (iv) In the second half of the twentieth century, the first timber concessions were granted in the area. Presently, 83% of the UBRB is covered by forests, of which 56% is designated for sustainable harvest in the Imataca Reserve. About 12% of the area is savanna and cattle pasture. The remaining 5% is covered by garden plots, houses and urban infrastructure. Immigration is accelerating forest conversion. Timber extraction, mining and cattle ranching are the most profitable land uses; agriculture remains a small-scale subsistence activity. Loss of forest cover is very high on the privately owned and municipally owned lands, while continuous cover is better preserved inside the federally owned IFR. Expanded mining—not only for gold, but also for diamonds and other minerals—and timber extraction represent the greatest threat to the area.

Presently, the population of the UBRB is culturally diverse and uses of the biotic and abiotic resources of the ecosystem are correspondingly diverse. Differences in LU practices, combined with different ways of thinking about and perceiving the natural surroundings, spawn conflicts, some of which are severe enough to threaten the ecological, economic and social sustainability of the UBRB (Mansutti et al. 2000). Irrespective of cultural and cognitive differences, strong material connectivity between the human and biotic communities in the UBRB prevails. Local natural systems supply local peoples with food, clothing, shelter and medicines, and therefore the majority of basic human material needs are locally satisfied. Many of the indigenous communities have negligible access to markets and imported resources. Creole communities do have that access, but most also rely on the local natural systems for many of their resource needs. Thus, the material connectivity is relatively high.

For purposes of a biocomplexity-based biodiversity management strategy, it is important to consider flora and fauna species that are most frequently used for human subsistence and local commerce. These species might serve as surrogates for biodiversity from the point of view of those who depend on them. We have identified non-timber forest products (NTFP) by means of personal interviews conducted in 310 homes, using a semi-structured questionnaire. A total of 94 species in 34 taxonomic families and 84 genera were identified in this survey. Uses include medicinal (35%), food (32%), fibre and handcrafts (13%), animal feed (11%), dyes (7%) and ornamentals (3%). A substantial number of NTFP species used by Creole habitants have been introduced from other regions: at least 14% of the species are nonnative; about half of these are from Mesoamerica and/or the Caribbean and about a third are from Southeast Asia. The trees used most frequently are: mango (Mangifera indica), onoto (Bixa orellana), jobo (Spondias mombin), guamo (Inga sp.), guayabo (Psidium guajava), pardillo (Cordia alliodora), guanábano (Annona muricata), purgo (Manilkara bidentata), quina (Angostura trifoliata), aguacate (Persea americana), tacamajaca (Protium sp.), rosa de montaña (Brownea sp.), cedro amargo (Cedrela odorata), algarrobo (Hymenaea

courbaril), mamón (Melicoccus bijugatus), tampipio (Couratari multiflora), pomalaca (Syzygium malaccense), corozo (Acrocomia aculeata) and merey (Anacardium occidentale) (Figueroa & Castilla 2006).

Although the population density is relatively low in the UBRB, pressure exerted on the fauna is high. There, fishing and hunting are the deeply ingrained traditions for generations immemorial. From our recent surveys, 38% of interviewed residents hunt to satisfy their basic needs, while 35% also hunt commercially. Of the total interviewed, only 27% do not hunt. A substantial proportion of families (74%) consume game for animal protein. The game is mostly mammalian. The species subject to the greatest hunting pressure are white-tailed deer (Odocoileus virginianus), locho deer (Mazama gouazoubira), lapa (Agouti paca), danto (Tapirus terrestris) and morrocoy (Geochelone denticulada). Birds are hunted in lower proportion and are mainly paujies (Pauxi pauxi) and pavas (Penelope sp.). Another subsistence activity for animal protein is fishing in rivers and lakes by 57% of the population. Guabina (Hoplias malabaricus) are preferred by 53% of those who fish (Navarro 2005).

Most local people understand the adverse consequences of declining animal numbers and disappearing faunal species. For about two-thirds of the UBRB's population (both indigenous and nonindigenous), the medicinal resources of the forest are very important, so much so that they consider them to be irreplaceable and not appropriately valued economically in a monetary metric. Water quantity and quality are also highly valued, the latter especially in those communities afflicted with water-borne diseases (Delgado et al. 2005: Sánchez-Torres & Rosales 2006).

The psycho-spiritual connectedness of the peoples of the UBRB to the natural systems is also high, especially among the indigenous groups who are invested in local natural systems for more than their basic material needs. The natural environments that they inhabit are vital to their personal and cultural identity, symbolic meaning and religious practice. Both indigenous and some Creole peoples have developed ways of life that are remarkably in sync with the UBRB's ecosystems. Their psycho-spiritual connection to the UBRB is expressed in complex religious and symbolic schema and in their very detailed vernacular ecological knowledge of the natural resources of the region (Colchester 2003).

As in the BT, so in the UBRB, biodiversity preservation hinges on federal ownership and stewardship of forest reserves. However, unlike the BT, which was largely uninhabited prior to settlement and resource exploitation in the nineteenth century, the UBRB has been inhabited by humans for many centuries. Just as the low degree of material connectivity of the contemporary denizens of the BT suggested a conservation strategy, so the high degree of material connectivity of the denizens of the UBRB suggests another: the subsistence practices of the indigenous peoples have been more compatible with the UBRB's biodiversity than recently expanding cosmopolitan LU/LC changes. Thus, in addition to protecting the forest, the government of Venezuela recognizes the importance of protecting the rights of indigenous peoples to continue practising their traditional ways of life and livelihoods.

4. THE CAPE HORN ARCHIPELAGO

At the extreme southern tip of South America lies an extensive and remote area of temperate forests—the Magellanic sub-Antarctic forests, recently identified as one of the world's 37 most pristine ecoregions (Mittermeier et al. 2002). This region is one of the only extensive areas in the world whose forests remain unfragmented (Silander 2000). The temperate forests of the Americas and much of the rest of the world have suffered even greater and much more prolonged anthropogenic disturbance than their tropical counterparts, because they were the primary targets of colonization by European immigrants during the past few centuries (Crosby 1972). The Cape Horn Archipelago (CHA) remained free of modern human impact thanks first to its geographical isolation and later to the presence of a military reserve controlled by the Chilean navy (Rozzi et al. 2004a). Nevertheless, until recently, the CHA was not identified as a priority for conservation. Upon organizing and detailing the attributes indicated here, however, the Cape Horn Biosphere Reserve was created in 2005 under the auspices of the UNESCO Man and the Biosphere Programme (Rozzi et al. 2006).

The CHA is situated south of Tierra del Fuego, between 54–56° S and 72.5–66.5° W and comprises an area of nearly 50 000 km²—approximately one-third of which is land and two-thirds water. The climate is moderated by isothermal oceanic conditions, providing an average temperature of 6°C, with means of 9 and 2°C for the warmest and coldest months, respectively. A sharp rainfall gradient runs from west to east due to the rain shadow cast by the Fuegian Andes: annual rainfall is 4000 mm on landforms exposed to the westerly winds from the Pacific and only 470 mm on the eastern side of the cordillera (Rozzi et al. 2004a).

The combination of a sharp rainfall gradient and the steep topography generates a mosaic of dramatically contrasting biotic communities. Forests dominated by Nothofagus spp.—southern beech—characterize the temperate zones of the Southern Hemisphere, including Tasmania, Australia and New Zealand, as well as southern South America, a legacy of old Gondwanaland (Veblen et al. 1996). These beech forests segregate into types determined by moisture and elevation: (i) sub-polar Magellanic evergreen rainforests grow along the coastlines in areas with 1000-4000 mm of annual rainfall, and are dominated by an endemic species Nothofagus betuloides, together with subdominant evergreen species, notably Winter's bark (Drimys winteri), which has a Neotropical origin; (ii) deciduous beech forests, which grow in areas of good drainage and less than 1000 mm annual rainfall, dominated by Nothofagus pumilio; and (iii) mixed beech forests, which combine the dominant evergreen and deciduous Nothofagus spp. and cover areas that are more sheltered with relatively good drainage. Mixed forests provide the preferred habitat for cavity-nesting birds, such as the Magellanic woodpecker (Campephilus magellanicus),

the largest woodpecker in South America. Above the timber line, a significant number of lichen species grow on the rocks, together with shrubs and krummholtz tree formations. Extensive wet areas of the CHA are dominated by the Magellanic tundra complex, which include peatlands, dominated by Sphagnum mosses; cushion-plant bogs in saturated places with poor drainage, dominated by species of Astelia, Azorella, Laretia and Bolax; and wetlands, dominated by the rush Marsippospermum grandiflorum. Finally, glaciers extend over a large portion of the Darwin mountain range and Hoste Island. In short, the Cape Horn region is famous for its mosaic of pristine biotic communities of multiple biogeographical origins and contrasting appearance (Rozzi et al. 2006).

The Cape Horn region is also of great cultural value, principally because it constitutes the ancestral territory of the Yahgan, the world's southernmost ethnic group (McEwan et al. 1997). Nomadic hunters, fishers and gatherers, the Yahgan canoed the channels of the archipelago, leaving behind a remarkable archaeological and cultural legacy (Gusinde 1961; Rozzi et al. 2003b; Rozzi 2004). More than five cultural depositions per kilometre have been found along the coastlines of CHA islands that have been studied, thus constituting one of the densest and best-preserved congeries of archaeological sites in the world (Rivas et al. 1999; Alvarez et al. 2004). Among them are many 'wigwam hollows'—2–3 m high shell mounds within which the Yahgan built huts to shelter themselves from the strong winds and rains coming off the Southern Ocean. These structures are unique to CHA, not found among the remains of other canoe groups. The CHA also occupies a central place in the history of science, because Charles Darwin (1839) spent a significant amount of time there during his Beagle voyage. His encounters with the Yahgan—generically called Fuegians—were crucial for the development of his concepts of human evolution (Rozzi 1999; Rozzi et al. 2003a). Further, Cape Horn plays a major role in the history of sailing and navigation (Vairo 2001).

Human occupation of the CHA falls into four distinct historical periods: (i) the Yahgan had the region to themselves until 1850; (ii) Anglican missionaries and European colonizers moved in and stayed for a century; (iii) the Chilean navy made a strategic military reserve of the CHA for a half century (1950-2000); and (iv) 'development' of tourism and a fishery is filling the void left by the navy's withdrawal in the first decade of the twenty-first century. The indigenes of the archipelago were primarily marine foragers living on the coasts—as their extensive shell middens indicate—for at least 7500 years. Molluscs were a year-round staple, but they did not satisfy the Yahgan's energetic needs. Hence, they had to travel constantly in search of fish, birds, sea lions, sea otters, whales and terrestrial mammals. Associated with this nomadic, highly varied marine-terrestrial way of life, the Yahgan developed a complex cosmology and spoke a language with a vocabulary of more than 32 000 words (Rozzi et al. 2003a,b).

The Anglican missionaries introduced English instead of Spanish—the predominant colonial language in the rest of Chile—and established large ranches.

British vegetables were planted in kitchen gardens and British grasses were sown as fodder for Scottish sheep (Bridges 1949; Rozzi *et al.* 2004*b*). Sheep ranching became the mainstay of the colonial economy, as well as for the indigenous people who became employees of the haciendas. However, the colonial reach was never great and the marine interstices between islands constituted a barrier to dispersal—and so exotic plants in the CHA remain confined to the places where ranches were established (Rozzi *et al.* 2004*b*). On the other hand, colonists did transmit Old World pandemic diseases—mainly smallpox—to the Yahgan, which rapidly reduced their population from an estimated 3000 in 1855 to 70 in 1923 (Alvarez *et al.* 2004).

The Chilean navy created a base and the town of Puerto Williams in 1953. The formerly scattered population of the region soon concentrated in the new town. The navy also created pastures for their livestock (cattle, pigs and horses, as well as sheep) in addition to houses, schools, offices, docks and roads. However, more than 95% of the territory was managed as a military reserve—and thus also, by default, a nature reserve that protected the pristine ecosystems. In addition, respectively, in 1945 and 1967, the national parks of Cape Horn and de Agostini were created to protect 74% of Chile's Cape Horn County (Rozzi *et al.* 2004*a*).

During the first decade of the twenty-first century, however, even the southern extreme of the Americas is threatened by economic development—coming in two main forms, commercial fishing and ecotourism. In 2001, the Chilean navy opened three new maritime routes to facilitate tourism out of Puerto Williams, to which environmentally perceptive people are attracted owing to its proximity to one of the world's least humanly impacted redoubts. The burgeoning Cape Horn ecotourism industry faces the familiar conundrum of ecotourism everywhere-preventing the destruction of the very attributes that clients come to experience. Presently, the Yahgan live alongside navy personnel, public-services employees and the new entrepreneurs. Nevertheless, much of their ancestral knowledge of the biota survives. Unfortunately, the Yahgan are the least empowered group in the publicpolicy and economic-development decision-making processes (Rozzi et al. in press).

Until just a century and a half ago, both human material and psycho-spiritual connectivity to the CHA was at a maximum value among its indigenous inhabitants—who were, until then, its only inhabitants living in very nearly complete isolation from the rest of the world. After the British missionaries arrived in the area, both forms of connectivity diminished. As in Australia so in Cape Horn, the British engaged in 'acclimatization'—the systematic introduction of the familiar flora and fauna of England, doubtless for (misguided) aesthetic as well as for economic reasons (Williams & West 2000). Though increasingly dependent on translocated exotic plants and animals, local material connectivity remained high in this place remote from international markets between 1850 and 1950. Psycho-spiritual connectivity to the Cape-Horn landscape—at least in terms of religion and worldviewwas low among the British, and was diminished among the Yahgan to the extent that Anglican missionary work was successful and, more grimly, to the extent that the indigenous population was decimated by disease. The same is also true of the period of naval administration from 1950 to 2000.

Now that the Yahgan have become integrated into the larger Chilean and increasingly international culture that is taking root in the CHA, the level of human material connectivity to the region falls somewhere between the relatively low level in the BT and the relatively high level in the UBRB. For example, marine food resources continue to be extensively utilized locally. Presently, however, a real opportunity exists to enhance the psycho-spiritual connectivity to the region. Self-selecting ecotourists bring with them an international environmental ethic, aesthetic and spirituality in regard to which the CHA is preeminently satisfying. The new biosphere-reserve designation, the relatively new national parks, and the associated emergence of ecotourism provide, additionally, an opening and an infrastructure for the revival of Yahgan vernacular ecological knowledge, religious symbols and worldview as an interpretive medium for visitors. The biosphere-reserve approach to conservation recognizes and emphasizes the coupling of natural and human systems and is thus an ideal framework for biodiversity conservation here. As applied to the CHA, plans for developing ecotourism and a commercial fishery may be based on the Yahgan conceptual schemata, preserved in their language, and nomadic patterns of the traditional Yahgan way of life.

5. DISCUSSION

The layering of the comparatively new concept of biocomplexity over the now-familiar concept of biodiversity suggests a novel approach for using the past to manage the future. Many, if not most, of the world's natural systems interacted with human systems over many centuries (Messerli et al. 2000). Between the mass extinction event at the Pleistocene-Holocene boundary in the Americas and the relatively recent onset of indiscriminate mass extinction, the rate of extinction was relatively low during most of the Holocene—and thus the biodiversity of natural systems interacting with human systems remained relatively constant (Barnosky et al. 2004). Understanding the dynamics of past CNHS may enable stakeholders and policy makers to re-establish sustainable future CNHS dynamics. Certainly, stakeholders and policy-makers can draw on knowledge of the CNHS dynamics of the past in managing the biodiversity hotspots featured in this article.

For example, the US National Park Service, local chambers of commerce and real estate developers could, each for reasons of their own, play up the romantic CNHS past of the BT. Texans in general are enamoured of their frontier heritage and, even if the motive of those who promote it is crassly commercial, preserving a vestige of that heritage in the BTalligators along with legendary outlaw hideouts, redcockaded woodpeckers along with rednecks—is a viable conservation goal even in the face of the

apparently inevitable circumstance of accelerating residential and commercial development in the region. After all, an anti-littering campaign in the state under the quasi-patriotic slogan, 'Don't Mess With Texas', has been demonstrably successful (Erenkrantz 2006). However, the best that can be hoped for in the BT appears to be a modest expansion of the fragmented protected areas in a matrix of up-scale residential and commercial development hopefully including extensive green spaces and buffer zones-styled and sold as ecologically and environmentally designed. Thus, the BTNP would become a kind of outdoor biodiversity museum in a pleasant, largely forested exurban setting.

In the UBRB and, more widely, in the IFR in Venezuela, key to preserving the biodiversity of the region is ensuring the rights of the indigenous peoples to continue to practise their biodiversity-compatible traditional life ways and livelihoods. In short, preserving the biodiversity of the region turns on preserving its historic biocomplexity. While in the United States, public property rights are as vigorously enforced as private, in Venezuela extra-legal cattle ranching, timber harvesting and mineral mining often encroach on designated reserves. Hence, vigorous enforcement of public property rights is also a key to preserving biodiversity in the UBRB. In the CHA, the Yahgan no longer live as their ancestors did. Hence no traditional life ways and livelihoods remain to be protected. While Yahgan material culture is all but extinct, Yahgan cognitive culture remains recorded in the Yahgan-English dictionary—compiled in the nineteenth century by Thomas Bridges, an Anglican missionary—and survives in the living memories of the contemporary Yahgan and should be actively cultivated and conserved. It represents an important tool and resource in the evolution of an ecologically and environmentally responsible ecotourism industry.

Further, attention to biocomplexity provides a deeper insight into the conceptual ambiguity of biodiversity. Biodiversity is perceived through cognitive complexes and these vary both between and within cultures. In short, biocomplexity relativizes the concept of biodiversity. The absolute biodiversity of even the smallest landscape unit cannot be measured, if we take into account all five biological kingdoms—monera, protista, fungi, plants (vascular and non-vascular) and animals (vertebrates and invertebrates).

Thus, as we noted in §1, the biodiversity of various landscape units is necessarily assessed by means of surrogates (Sarkar 2002). And, as also noted, the most commonly used surrogates are vascular plants and vertebrate animals (Myers et al. 2000). We are vertebrate animals ourselves and are evolved to be aware of organisms of similar size and individuality. Unaided by microscopes, we cannot even directly perceive monera and protista. However, of the macroscopic biota, insects make up the bulk of all species (Myers et al. 2000). In The Descent of Man, Darwin (1871) asked his readers to imagine how 'right or wrong' might appear to 'hive-bees'. Similarly, it might be instructive to imagine how biodiversity might appear to a scarab and what class of species a beetle might choose to represent total biodiversity. If

we shift cognitive lenses and try to compensate for our vertebrate/vascular bias, hitherto invisible reservoirs of biodiversity may snap into focus.

One of our case studies illustrates this shift. In Chile, the highest diversity of forest types and tree species richness, the maximum concentration of endemic woody genera, and the maximum species richness of native mammals, amphibians and freshwater fishes are found within a latitudinal range of 35–40° S. However, more than 90% of protected lands in Chile are concentrated at high latitudes (greater than 43°S) outside the richest area of biodiversity as represented by woody plants and vertebrate animals. Therefore, paradoxically, the amount of land in parks and reserves in Chile is inversely correlated with the country's species richness and endemism—when the vascular flora and vertebrate fauna are considered as indicator or surrogate groups (Armesto et al. 1998).

However, when non-vascular flora are selected as indicators of biodiversity, a different picture emerges: more than 60% of the known non-vascular plant species of Chile grow exclusively south of 40° S, and the Cape Horn region itself hosts 67% of Chile's 549 liverworts and 58% of its 778 mosses (Rozzi et al. in press). Moreover, in Cape Horn, non-vascular outnumber vascular-plant species 818 to 773, a ratio dramatically contrasting with the worldwide ratio of 15 000 to 272 655 (approx. 1 to 20), respectively. Further, 5% of the world's bryophytes are found in less than 0.01% of the Earth's land surface at the southern tip of the Americas. By these measures, the Cape Horn region is indeed a floristic hotspot. These considerations led to a focus on Cape Horn as a priority site for conservation in Chile and provided a major reason for its designation by UNESCO as a biosphere reserve (Rozzi et al. 2004a).

Bias in recognizing the richness of non-western cultural traditions and indigenous knowledge rivals that in recognizing non-vascular/invertebrate biodiversity. Even Darwin, famed for his powers of observation, erred in his first perception of Yahgan culture and language. In Voyage of the Beagle, Darwin (1839) described the Yahgan language as a scarcely articulate 'chuckling kind of noise, as people do when feeding chickens'. Many years later, Darwin revised this assessment after he learned of the Bridges Yahgan-English dictionary, which included more than 32 000 words. That dictionary made such a strong impression on Darwin that he changed his initial low estimation of the intellectual attributes of the Fuegian-Yahgan. His revised assessment of Yahgan language and culture influenced his evolutionary arguments in favour of the similarities among human ethnicities and races in The Descent of Man (Rozzi 1999; Rozzi et al. 2003a).

Biocomplexity studies represent a powerful new approach to understanding and managing biodiversity. We do not, however, propose this approach as a substitute for the more familiar universal approach of establishing biodiversity preserves, but rather as a complement. All the three of the hotspots reviewed here are protected to one degree or another by preserves of one sort or another: parts of the BT by designation as a US National Park Preserve, which is

also a UN biosphere reserve; parts of the UBRB by designation as part of a forest reserve (the IFR); and parts of the CHA by designation as national parks and a UN biosphere reserve. The universal approach of legalized protection can, however, engender indifference or resentment if not complemented by systematic attention to the human aspect of CNHS.

6. CONCLUSION

Now that the wilderness myth has been debunked, the baby should not be thrown out with the bathwater (Callicott & Nelson 1999). Even in temperate North America extensive patches of uninhabited, little-impacted landscapes existed. The BT was one such place. On the other hand, our South American study sites were inhabited by indigenous people throughout most of the Holocene, but in numbers and ways that were compatible with the continued existence of their biota's non-human components. The swidden agricultural practices of the indigenous peoples of the UBRB are a case in point. Understanding past CNHS, as this example indicates, can serve as a point of reference for their future management. Further, foregrounding human systems and their inherent cultural component makes us aware that natural systems are inescapably apprehended through culturally variable cognitive lenses. Such a realization invites us to assess biodiversity in more ways than one. By changing cognitive lenses, new reservoirs of biodiversity may be revealed, as they are in the CHA.

Complementing the establishment and expansion of parks and reserves in the hotspots reviewed here, our biocomplexity approach to biodiversity conservation is based on the biocultural history and assessment of the nodes of CNHS connectivity in each region—as well as on the potential for influencing public-policy and private land-use decision making afforded by CNHS modelling and simulation. In the BT, the low material connectivity and relatively high potential for psycho-spiritual connectivity suggests a strategy of designing and marketing residential and commercial development that preserves the historic romance and mystique of the region, which is so closely associated with its overall forested character and species and landscape-level biodiversity. In the UBRB, the relatively high material and psychospiritual connectivity of its indigenous populations suggests a strategy of protecting the rights of those people to pursue their traditional livelihoods and life ways, which so thoroughly depend on such a wide variety of plant and animal species that can serve as vernacular surrogates of biodiversity. In the CHA, the middling degree of contemporary material connectivity in combination with an increased understanding and appreciation of the traditional patterns of subsistence and the rich cognitive culture of the Yahgan provide historic points of reference and interpretive schemata for the emerging fishing and ecotourism industries. That interpretive framework can further expand and enrich the concept of biodiversity itself for visitors to the region and, more generally, for conservation biologists.

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