Gaia's Handmaidens: the Orlog Model for Conservation Biology

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Abstract: The Gaia bypothesis, which proposes that Earth's biota and material environment form a selfregulating system, has been influential in conservation biology, but it has not translated into specific guidelines. Proponents of phylogenetics and ecology often claim primacy over the foundations of conservation biology, a debate that has deep roots in philosophy and science. A more recent claim is that conservation efforts should protect evolutionary processes that will allow diversification. Phylogenetics, ecology, and evolution all have legitimate roles in conservation, when viewed in a temporal perspective. Phylogenetic studies identify the bioheritage of past species radiations, ecology preserves the life-support systems for these lineages in the present, and evolutionary processes allow adaptation of these lineages to novel challenges in the future. The concept of temporal domains in conservation (past, present, future) has an appropriate metaphor in the Norse worldview known as the Orlog. In this body of mythology, three sisters tend the tree of life and fend off a dragon gnawing at the roots. The names of these sisters, Urd, Verdandi, and Skuld, translate to Past, Present, and Future. In Viking mythology, the threads of life cannot persist without the cooperation of these sisters. In the science of conservation biology, they represent the bandmaidens of Gaia-three scientific disciplines that can succeed only with a spirit of familial cooperation.

Key Words: bioheritage, ecology, evolution, marine protected areas, phylogenetics

La Servidumbre de Gaia: El Modelo de Orlog para la Biología de la Conservación

Resumen: La hipótesis de Gaia, que propone que la biota terrestre y el ambiente material forman un sistema autorregulado, ha influido en la biología de la conservación, pero no se ha traducido en directrices específicas. Los proponentes de la filogenética y la ecología a menudo demandan la primacía sobre las bases de la biología de la conservación, un debate que tiene profundas raíces en la filosofía y la ciencia. Un enunciado más reciente es que los esfuerzos de la biología de la conservación deben proteger procesos evolutivos que permiten la diversificación. Tanto la filogenética, la ecología y la evolución tienen papeles legítimos en la conservación, al verla en una perspectiva temporal. Los estudios filogenéticos identifican el biopatrimonio de las radiaciones de especies pasadas, la ecología preserva a los sistemas de soporte de la vida para estos linajes en el presente y los procesos evolutivos permiten que estos linajes se adapten a cambios en el futuro. El concepto de dominios temporales (pasado, presente y futuro) en conservación tiene una metáfora adecuada en la cosmovisión Nórdica conocida como el Orlog. En este cuerpo de mitología, tres bermanas atienden el árbol de la vida y lo defienden de un dragón que roe sus raíces. Los nombres de estas bermanas, Urd, Verdandi, y Skuld, se traducen como Pasado, Presente y Futuro. En la mitología vikinga, los bilos de la vida no pueden persistir sin la cooperación de estas bermanas. En la ciencia de la biología de la conservación, representan a la servidumbre de Gaia - tres disciplinas científicas que solo pueden tener éxito con un espíritu de cooperación familiar.

Palabras Clave: áreas marinas protegidas, biopatrimonio, ecología, evolución, filogenética

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Introduction

The ancient cultures of northern Europe, epitomized by the Vikings, have a history steeped in blood and a mythology to match this colorful past. Humanity's relationship with the natural world also has a violent history, in which the axe falls not on hapless Saxons but on the organismal lineages that define our biological heritage. Recent paleontological evidence demonstrates that this tradition runs deep and wide, beginning before recorded history and culminating in the current wave of extinctions (Diamond 1989; Kerr 2003). In this increasingly desperate fray, three biological disciplines claim primacy over the conceptual foundations of conservation: phylogenetics, ecology, and evolution.

Phylogeneticists claim that the centerpiece of conservation is the taxon. In this view, the focus of conservation is the organismal lineage: subspecies, species, genera, or deeper taxonomic categories (Forey et al. 1994; Pennock & Dimmick 1997; Faith 2002). An important corollary is that conservation priorities can be ranked according to phylogenetic depth: the highly distinct coelacanth (a lobe-finned fish whose roots fall close to the origin of tetrapods) would be a much higher priority than a cichlid fish from the species flocks of East Africa.

Ecologists often maintain that conservation efforts must address ecosystem health rather than the protection of individual taxa (Grumbine 1990; Schmidt 1996). From this perspective, ecosystems are the life-support systems for each species, as they are for all contemporary life on Earth. If ecosystems are healthy, individual taxa are at lower risk.

The dispute between systematic and ecological views has sharpened in the last decade, with proponents of each discipline claiming primacy (Noss 1996; Wheeler & Cracraft 1996; Dimmick et al. 1999; Posadas et al. 2001; Redford et al. 2003; Faith et al. 2004). In this heated environment, there is a danger that conservation agendas will bias the interpretation of scientific results (Bowen & Karl 1999; Karl & Bowen 1999).

A relatively new point of view is the evolutionary perspective, prompted by the applications of genetics in conservation. Under this view, conservation efforts must be dedicated to preserving the processes of speciation and adaptation (Frankel 1974; Soulé & Wilcox 1980; Lande & Shannon 1996; Lynch 1996; Moritz 2002). In the simplest terms, genomic diversity is the currency of evolutionary radiations, and conservation priorities should lie not with phylogenetically divergent taxa but with emerging species and evolutionary novelties that hold the promise of future biodiversity. Speciose lineages, or those with ongoing evolutionary radiations, are viewed as conservation priorities (Erwin 1991). One corollary of this viewpoint is that highly distinct taxa (living fossils) may be the last remnants of previous evolutionary radiations, dead ends that should not be subject to intensive conservation efforts.

Hence the evolutionary perspective appears to contradict the priorities of the phylogenetic school: evolutionary biologists would preserve the speciose cichlids rather than the ancient coelacanths.

We propose a resolution of the contest between phylogenetics, ecology, and evolution, based on a cosmological metaphor, the Orlog, or worldview of Viking mythology. In an extension of the Gaia hypothesis, which emphasizes the interaction of living organisms to maintain life on Earth, the Orlog mandates specific roles for the three scientific fields that dominate conservation biology.

The Orlog

Is conservation the domain of phylogenetics, ecology, or evolution? A general response, implicitly borne by most conservation biologists, is that none of these disciplines alone is sufficient (e.g., Meffe & Carroll 1997). It is clear that conservation cannot be reduced to a prix fixe menu with a choice of landscapes, taxa, or genotypes. A more exact answer begins with the recognition that the systematic perspective is inherently focused on the past, with a goal of identifying the successful products of previous evolutionary radiations. The ecological perspective is based in the present because contemporary habitats are the focus for conservation efforts. The evolutionary view looks toward maintaining biodiversity in the future. When viewed from this temporal perspective, the three biological disciplines that claim domain over conservation are not conflicting; rather, they address three essential components: the preservation of the threads of life as they arrive from the past (phylogenetics), abide in the present (ecology), and extend into the future (evolution). In this temporal perspective, the three disciplines have complementary rather than competing roles in conservation (Bowen 1999).

The concept of life as a thread winding through time has several antecedents in the mythology of Indo-European cultures; the best known are the three fates of Greek pantheism. In this version, three women weave a tapestry in which each life is a single thread. A break in the strand means death, and neither god nor man can stay the hand that cuts the thread.

Less well known, but perhaps a more appropriate metaphor for conservation biology, is the worldview of the Norse culture, which thrived around 800-1100 AD. In the body of mythology known as the Orlog, there is a world tree named Yggdrasil (pronounced IG druh sil, http://www.earthisland.org/yggdrasil/) upon which all life depends. Dark forces attack the tree, including a mysterious fungus and a dragon that gnaws at the roots. Three sisters labor against the forces that could overwhelm the tree. Their names are Urd, Verdandi, and Skuld, which translate to Past, Present, and Future. These sisters, known as the Norns, are essentially Gaia's handmaidens, in an explicit temporal framework that matches the

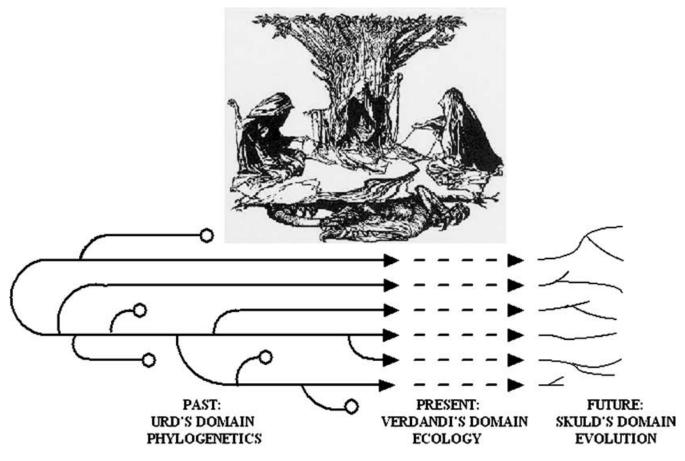


Figure 1. An artistic rendition of the Norns, with a dragon encircling the roots of the world tree. The phylogenetic tree is based on the evolutionary bistory of sea turtles as inferred from molecular-sequence comparisons (Bowen & Karl 1996; Dutton et al. 1996). Hypothetical extinctions are indicated as terminal circles. The process of conserving sea turtles may start with phylogenetic studies to identify the products of past phylogenetic radiations. Subsequently, ecologists identify the key babitat features that allow sea turtles to survive and thrive in the present. Finally, evolutionary biologists identify the raw materials for future prosperity and diversification. (The drawing of the Norns is an illustration by Arthur Rackham from The Ring of the Niblung/Siegfried and the Twilight of the Gods, by Richard Wagner; translated by Margaret Armour; Abaris Books, New York, 1910. Scanned at sacred-text.com, March 2003 by J. B. Hare.)

conservation roles of phylogenetics, ecology, and evolution (Fig. 1).

The roles of phylogenetics and ecology in conservation are well developed and widely accepted. The preservation of biodiversity (Urd's domain) depends on systematic and taxonomic knowledge, and it is inevitable that Verdandi's domain, concerned with contemporary habitats, will consume the majority of resources dedicated to conservation. In contrast, the evolutionary component of conservation (Skuld's domain) is the least resource intensive. This may be appropriate because divining the future of species is a fool's errand (Bowen 1998). Even when we can identify emerging species, we cannot predict their success. Hence, Skuld may be the quietest of Gaia's handmaidens, and the least understood (Table 1), but she cannot be neglected. Debate continues on the nature of the genetic diversity that may be most relevant to conservation programs (Lynch 1996; Storfer 1996), but evolutionary principles are already an important aspect of management programs (Zimmer 2003), perhaps most prominently in fighting the pernicious effects of inbreeding in small populations. Furthermore, selective pressures created by human alterations can induce rapid genetic responses (Law 2000; Palumbi 2001*a*). Given such pressure, it is important to incorporate studies of the evolutionary mechanisms of adaptation and speciation-from reproductive isolation to quantitative genetics-into conservation programs (Crandall et al. 2000; Fraser & Bernatchez 2001; Ashley et al. 2003).

The Orlog draws distinctions between systematics, ecology, and evolution, but it does not mandate that these fields operate in isolation. Indeed the concept of sisters, closely related entities cooperating to preserve the tree of life, is an apt model for the three biological disciplines.

Table 1. Systematic, ecological, and evolutionary components of conservation.	Table 1.	Systematic,	ecological, and	l evolutionary	components of	conservation.
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Species	Range	Phylogenetic distinction	Ecological importance	Evolutionary potential*
Horseshoe crab				
Limulus polyphemus	North Atlantic	high	high	low
Coelacanth fish				
<i>Latimeria</i> sp.	Indo-Pacific	high	low	low
Cichlid fish				
Haplochromis sp.	Africa	low	variable	high
Leatherback turtle				
Dermochelys coriacea	Oceanic	high	medium	unknown
Map turtle				
<i>Graptemys</i> sp.	southeastern U.S.	low	medium	high
North Atlantic right whale				
Eubalaena glacialis	North Atlantic	medium	low (at present)	low
Florida panther				
Puma concolor	southern Florida	low	high	low
Longleaf pine				
Pinus palustris	southern U.S.	low	high	unknown
Pitcher plant				
Saracenia purpurea	North America	high	high	low

*The category of evolutionary potential is speculation based on the presence or absence of recent evolutionary radiations.

Just as phylogeneticists and ecologists work together to discover and preserve biodiversity hotspots, we recognize that the fields of ecology and evolution must also go hand in hand. Ecosystem diversity can be a driving force in evolutionary diversification (Schluter 2000), and the maintenance of ecological integrity and diversity may be the surest way of retaining the evolutionary potential of emerging species.

The Gaia hypothesis, named for the Greek goddess who conjured the living world from chaos, states that Earth's surface is different from that of its neighboring planets, Mars and Venus, and it is the interaction of living organisms with Earth's atmosphere that maintains this distinction (Lovelock 1972; Margulis & Lovelock 1974; Margulis 1998). In this view, "the organisms and their material environment evolve as a single coupled system, from which emerges the sustained self-regulation of climate and chemistry at a habitable state for whatever is the current biota" (Lovelock 2003). Yet the Gaia hypothesis and Orlog approach must look beyond the present day to incorporate biological processes over deep time: the Norse world tree, from roots to branches, represents our planet's bioheritage, encompassing our most distant common ancestor and the geminate species emerging today (Fig. 1).

The Orlog model addresses a fundamental limitation in applying the Gaia hypothesis to conservation issues. As originally proposed, the Gaia hypothesis of a living (selfregulating) planet includes no specific role for humanity as a cause of the extinction crisis or as a force for intervention. Indeed, the primary architects of the Gaia hypothesis have maintained that it is beyond human means to regulate the biological processes of our living planet. We agree that humanity cannot control the processes that make Earth a living planet, but the role of humanity in modifying these processes is undeniable. In our Orlog model, the dragon gnawing at the roots of Yggdrasil is a human creation, whereas the scientific institutions of phylogenetics, ecology, and evolution (and especially the agencies that implement these sciences) are the sisters protecting the world tree.

The Norse invocation of three sisters, winding the threads of life from past to future, can invoke a sense of predestination or inalterable fate. Indeed, the northern Europeans believed that their ultimate fate was set at birth, and nothing could alter the length of the life thread set by the three sisters. The Norse, however, also believed that personal choices and actions could determine spiritual and material well-being. Under the Orlog mythology, a person was not free to do anything, but he or she was not locked into a predetermined set of events either (Bauschatz 1982). Within the boundaries set by the gods, humans could accomplish much by personal choice. This combination of unalterable circumstances and personal accomplishment translates readily into the Orlog model for conservation biology. Humans cannot control Gaia, the living Earth, but we are certainly capable of damaging it. We can also mend it.

Resolving Conservation Priorities

The Orlog unites several concepts in conservation biology, but how are Gaia's handmaidens relevant to practical wildlife management? Consider the case of the Florida panther, originally thought to be one of 15 subspecies of puma, *Felis concolor*, in North America (Young & Goldman 1946). By the 1980s the sole remaining population of the panther was beset by declining numbers, severely

reduced genetic diversity, and a degraded habitat (Roelke et al. 1993). Wildlife managers had to make a choice between preserving the Florida panther as a unique taxon (the phylogenetic priority) or restoring panthers as a significant part of southern Florida's trophic web (the ecological priority). In this case, managers chose the latter priority and augmented both numbers and genetic diversity by introducing pumas from Texas. Although the Florida panther as a distinct taxon has been permanently corrupted, the ecological role of top predator has been partially restored. In weighing both taxonomic and ecological priorities, wildlife managers made a case-specific decision based on elements of the Orlog model.

Although such transplantations should be considered only as a last resort, the issue of managing genetic interchange may require an increasing role for evolutionary biologists. Many terrestrial carnivores have been reduced to fragmented, often dwindling populations. As metapopulations are disrupted, transplantation may be essential to supplement reduced populations and promote genetic health. This management option may not require many individuals; Vilà et al. (2003) documented the recovery of an isolated wolf population following the arrival of a single immigrant.

In the panther's case, the priorities of phylogeny and ecology came to the forefront, with less attention given to evolutionary consideration. However, a three-part assessment of conservation priorities, as indicated by the Orlog model, can inform decisions for other taxonomic groups. For example, the conservation of sea turtles (Fig. 1) can follow a three-step pattern: (1) a phylogenetic and taxonomic foundation identifies the divergent lineages that require protection; (2) ecological information identifies key habitats and trophic interactions across the life stages of each lineage; and (3) an evolutionary appraisal identifies the potential raw materials for future diversification and emerging species.

Ecosystem conservation often emphasizes the protection of contemporary conditions. Yet retrospective data, including paleoecological reconstructions and genetic surveys, can identify the causes of population declines and set goals for restoration and management (Jackson et al. 2001; Roman & Palumbi 2003). Ecosystems, like genomes, are always changing. Nowhere is this more apparent than in the ocean, where ecosystem regime shifts can occur on timescales from months to millennia (Lecomte et al. 2004). In the next section, we argue that the Orlog metaphor can guide the design of protected areas in the ocean, the most hotly debated context for wildlife reserves.

Designing Marine Protected Areas

The Orlog model can guide the design of wildlife reserves by defining goals in three general categories: endangered species preservation, ecosystem integrity, or evolutionary potential. All three goals are relevant to the design of marine protected areas (MPAs), although the third is seldom considered. In practice, most reserves are designed to preserve ecosystem diversity or enhance fisheries (Palumbi 2001*b*; Hastings & Botsford 2003). Recent field studies have confirmed the efficacy of MPAs for these ecological goals (Roberts et al. 2002; Friedlander et al. 2003), and the research agenda has shifted toward making reserves more effective. Size is a particularly pressing issue; estimates range from 10% to 50% of a particular area to show substantial benefits (Botsford et al. 2003; Hastings & Botsford 2003).

Whereas most reserves are based on ecological criteria, MPAs also serve the goal of preserving organismal lineages, and successful examples range from the calving grounds of seals to the migratory corridors of sea turtles (Norse & Crowder 2004; Sobel & Dahlgren 2004). The priorities of both Urd and Verdandi are apparent in the corresponding requirements of MPAs.

The primary difficulty with MPAs is that few marine species will complete their life history within the boundaries of a protected area. How can we design reserves for species that traverse hundreds or thousands of kilometers in the course of a lifetime? Most reef organisms have a pelagic larval stage, so their life cycle may include a period of weeks or months in the open ocean. Although this stage is not a conservation concern, postpelagic juveniles are susceptible to disturbances such as trawling (Watling & Norse 1998). In these circumstances, MPAs that include juvenile and adult habitat of coral reef species would seem to address the Orlog mandate for maintaining intact ecosystems. Unfortunately, this solution does not apply to highly migratory species such as whales, tunas, and sea turtles. The gray whale (Eschrichtius robustus) population that breeds in Baja California feeds in Alaska and migrates across the entire Pacific coast of the United States and Canada. Several species of tuna (Thunnus spp.) reproduce and mature in the open ocean while migrating across thousands of kilometers. Marine protected areas based on individual ecosystems will not meet the conservation requirements of these species. In this case, the emphasis must shift from ecosystem-specific to taxonspecific management programs including harvest restrictions and the protection of vulnerable life stages and critical habitats (Bowen et al. 2005).

Finally, how can evolutionary priorities contribute to the design of MPAs? In the earliest planet-wide summaries of marine biogeography, Eckman (1953) and Briggs (1974) identified areas of high species diversity, most notably among the reefs of the Indo-West Pacific region, as the wellspring that provides new species to other areas. Recent surveys of reef fish distributions and rangewide surveys of genetic diversity provisionally support this model of species production (Briggs 2003; Mora et al. 2003). If this model is correct, the center of the Indo-West Pacific, besieged by overfishing and habitat degradation, is an enormous conservation priority. Skuld may be the quiet sister, but her message may ring with ever-increasing urgency: Conservation cannot succeed without channels for future biodiversity.

Conclusion

A focus on the individual species, habitat, or genetic diversity alone is not sufficient to achieve the goals of conservation. In shedding the limited perspectives of individual scientific disciplines, conservation biology is reemerging with the goal of preserving the intricate threads of life as they arrive from the past, abide in the present, and project into the future. We believe the Orlog model, which encompasses phylogenetics, ecology, and evolution, is useful in defining conservation goals and the expenditure of resources. It may also help resolve the tensions between conservationists and the general public by uniting scientific fields, intuitive beliefs about nature, and mythology. We must address the dragon at our feet, gnawing at the roots of the tree of life. Is this dragon made of human greed, apathy, or a draconic aspect of our evolutionary destiny? No matter the face, if it is not tamed then one more northern European icon may serve to illustrate the conservation dilemma: the Dutch boy, with a limited number of fingers to plug the dyke.

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