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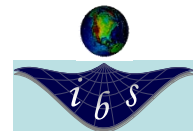
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cover: Replica of Chauvet cave art depicting aurochs, Woolly rhino, and wild horses. Original paintings are from the Aurignacian period, 31,000 yr BP. Picture by Thomas T., CC BY-SA 2.0 License. For more information about the aurochs (*Bos primigenius*) see the article by Carl Beierkuhnlein in this issue.

Placing phylogenetic diversity back on the evolutionary track

Conceptual frameworks relying on properties that are hard to measure are often challenging. A common solution is the use of proxies or surrogates for those properties. When molecular phylogenies became easily available and the conceptual framework by Webb et al. (2002) was published, many ecologists started to use phylogenies as proxy for ecological relationships. The study proposed straightforward hypotheses to infer community assembly processes by using phylogenetic information when trait information is not available, and rapidly became a seminal paper. The “phylogeny as a proxy to ecology” approach assumes that closely related species should share more similar features (e.g., ecological traits, habitats, environmental tolerances) than distantly related species, a statement that can be traced back to Charles Darwin (Webb et al. 2002). Indeed, the number of studies using this approach has quickly increased in recent years (Cianciaruso 2011), even in macroecological and biogeographical journals. Cianciaruso (2011) asked how macroecology and biogeography could benefit from phylogenetic diversity and how we could advance the theory by using novel approaches. An article recently published by Gerhold et al. (2015) presents an important contribution to answer these questions.

Gerhold et al. (2015) is a must-read paper for anyone thinking of using the “phylogeny as a proxy to ecology” approach because it highlights that phylogenies are not good proxies to ecology, and gives ideas on how ecologists and biogeographers can further connect community-level data to macroevolution. The authors challenge core assumptions that have been increasingly used in studies following the approach proposed by Webb et al. (2002). One of these assumptions is that phylogenetic clustering may be an outcome of trait clustering due to the action of environmental filters or that phylogenetic structure is mainly due to local and present-day processes. Since Webb and colleagues’ paper, several ecologists have used some of their assumptions without criticism

(Gerhold et al. 2015). For instance, macroecological studies have used phylogeny as a proxy (e.g., Cardillo 2011), which should be avoided considering the points made by Gerhold et al. (2015). It is important to note that other studies (e.g., Mayfield and Levine 2010) have raised some of the criticisms used by Gerhold et al. (2015), but the particular advantage of this new review is that it synthesizes the different criticisms to the “phylogeny as a proxy to ecology” approach.

But what does Gerhold et al. (2015) have to do with biogeography? Community ecologists and biogeographers have argued that community ecology and biogeography should be further integrated (Cavender-Bares et al. 2009, Cianciaruso 2011). Indeed, an attempt towards such an integration was one of the original aims of Webb et al. (2002; see their Figure 1), but it has been little explored over the years. Community ecology can benefit from biogeographic and phylogenetic approaches by putting history and evolution into the explanation for current patterns of biodiversity (e.g., community structure) as highlighted by Gerhold et al. (2015). Biogeography in turn can benefit from community ecology elucidating how local processes can feedback into regional processes, and helping explain how ecological processes shape the tree of life (i.e., phylogeny) and the current distribution of life on Earth (i.e., macroecological patterns) across evolutionary time via adaptation and other eco-evolutionary mechanisms.

Gerhold et al. (2015) argue that ecologists would improve their researches by considering phylogeny not as a mere proxy for ecology but rather by investigating how phylogenetic patterns can give insight into processes that drive species coexistence or are its outcome. Gerhold and colleagues made several points about the perils of using phylogeny as a proxy. We agree with their points. If species traits are already a proxy for functionality or species’ interactions (with other species or the environment), would it be safe to use a proxy of a proxy? We believe that it would not. We argue that ecologists

and biogeographers should be aware of the limitations of using phylogeny as a proxy of ecological distances, and avoid using this approach that has at least seven implicit assumptions that are weakly supported by the literature (Gerhold et al. 2015). Rather, they should think about possible historical and evolutionary explanations of their study patterns, and then elaborate clear hypotheses that may explain these patterns. Phylogeny is likely an irreplaceable tool for this purpose.

Gerhold et al. (2015) propose that phylogeny underlies the causes of current biodiversity patterns, which involves the assessment of the historical drivers of current community structure, or is a result of community assembly, which involves the evaluation of how ecological processes could scale up to broad scale patterns. Besides the future avenues highlighted by Gerhold and colleagues, some approaches have already shed light on the historical drivers of local diversity and thereby succeeded in moving towards an integration of ecology, biogeography and evolution. For instance: (1) linking alpha and beta phylogenetic diversities of local communities across distinct regions or biogeographic barriers (Graham and Fine 2008); (2) linking phylogenetic structure of local communities to characteristics of the regional phylogenetic pool (Gerhold et al. 2008, Lessard et al. 2012); (3) linking local phylogenetic structure to macro-ecoevolutionary processes such as speciation, extinction and long-distance dispersal (Davies and Buckley 2011); (4) linking beta diversity to species traits and information on biogeographic history of the study communities (Peixoto et al. 2014). These studies have built on ideas present in Webb et al. (2002), but used the phylogenetic patterns to make inferences about biogeographic processes rather than to assume that phylogenetic patterns are proxy to functional patterns.

In conclusion, Gerhold and colleagues placed phylogenies in ecology back on track by showing the limitations of currently widely used assumptions and by proposing future avenues of research for those aiming to understand biodiversity patterns through the lenses of historical and

evolutionary processes. We further argue that testing clear biological hypotheses in light of the interface between community ecology and biogeography will move biodiversity science ahead by enabling us to integrate explanations of the drivers of biodiversity patterns observed at several scales.

Marcos B. Carlucci, José Hidasi-Neto,
Fernanda T. Brum & Marcus V.
Cianciaruso

Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, Brazil.

marcos.carlucci@gmail.com;

<http://cianciaruso.wix.com/home>

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commentary

Ecotones – where biomes meet

The classification of biomes (or vegetation types) represents one of the most basic summaries of ecological units and provides part of the basis of biogeography. The first systematic continental biome map was a map of Africa produced by Schantz in 1923 (Küchler 1960). Since then, biome mapping has continually developed to inform biodiversity sciences. Initially such developments were mainly in the form of expert mapping, where vegetation scientists with good knowledge of the area being mapped, and often drawing on actual plant community data, drew the boundaries of biomes (Kent 2012). More recently, ever more reliance has been put on remote-sensing data, where algorithms are used to interpret satellite imagery to classify biome distributions (and other land use types; Xie et al. 2008).

With the concomitant development of other large-scale spatial datasets, such as of climate and soil, there has been an increased interest in the drivers of biome distribution, or elements of vegetation such as woody cover, at macroecological scales (e.g., Stephenson 1990, Greve et al. 2011, Campo-Bescós et al. 2013). Understanding what drives biome distribution is especially important in the face of global change, in response to which the distribution of biomes may be expected to shift. It has been suggested that if such shifts are to take place, the transition zones between vegetation types, i.e. the ecotones, would be most suitable for monitoring such changes (e.g., Berner et al. 2013; though see Kupfer and Cairns 1996). Ecotones are often also areas of high richness as they may harbour species from different biomes (e.g., van Rensburg et al. 2009), and may be important areas of gene flow and hybridization (Kark and van Rensburg 2006).

Against this background of the importance of ecotones, and a lack of attention historically afforded them (Kark and van Rensburg 2006), it is exciting that the South African Journal of Botany will shortly be releasing a

special issue dealing with “biome boundaries” in the South African context (Potts et al. 2015a). South Africa harbours a particularly high diversity of biomes (Mucina and Rutherford 2006), with some regions of high biome turnover across relatively small geographic distances (Fig. 1). This, together with the rich history for biome research in the country (Potts et al. 2015a), makes the region a natural laboratory to understand ecotones and their drivers.

The special issue presents work conducted at a range of spatial scales (Potts et al. 2015a), ranging from transplant experiments across biome boundaries (Esler et al. 2015) to works conducted across all biomes in the country. One of the country-scale studies examines the use and limitations of dynamic vegetation models in understanding the shifts of biome boundaries in response to climate change (Moncrieff et al. 2015), while another examines the extent to which ecotones can be also used to differentiate between alien plant composition (Rouget et al. 2015).

Other studies look at the role of soils in determining biome distribution (reviewed in Potts et al. 2015a). One of these used soil carbon isotope analyses to ask whether soil type might drive biome boundaries in a grassland-forest mosaic (Gray and Bond 2015). By examining the depth profile of carbon isotopes they concluded the opposite: that biome affects soil carbon. In the fire-prone grasslands, fires deplete nutrients, while nutrient build-up happens in forests, which are protected from fires. In this system, disturbances, rather than the abiotic environment, drive the position of ecotones.

A number of papers in the special issue look at changes in vegetation structure and boundaries through time using repeat aerial and ground-based photography (reviewed in Potts et al. 2015a). These studies, which could illustrate how shifts in biome boundaries occur (e.g., Masubelele et al. 2015), illustrate the im-

portance of long-term monitoring on ecotone environments for recognizing the effects of global change on biome distribution.

Of particular interest to the field of ecotone research will be a paper by Potts et al. (2015b), which reviews different manners in which ecotones are defined. Their review divides these into five different categories: field observations, including expert observations and more anecdotal accounts; modelling of correlations between environmental factors and biome characteristics; experimental approaches such as transplant experiments and controlled laboratory experiments where one or two factors can be systematically manipulated to determine their effect on plant growth; mechanistic modelling, which relies on simula-

tions of biomes based on a process-based understanding of its components; and finally, phylogenetic approaches, which seem to not be used to delineate biome boundaries as much as they utilize information about biome shifts within clades or diversification rates to understand the origin of biomes.

While this special issue particularly focuses on ecotone research within the South African context, it highlights a number of advances in the field, and illustrates a number of different approaches that can be utilized in the field of ecotone research, many of which will be of interest to biogeographers. Biogeographers already have a great interest in the drivers of biodiversity change across gradients, which is apparent from the many studies dealing with



Figure 1. Photo showing three biomes within a very short distance from one another at the Kranskop in KwaZulu-Natal, South Africa. The slopes on the right of the photo face north-west, exposing them to warm conditions resulting in the occurrence of drier savannas. The grasslands on the top of the ridge are burnt regularly and could be prone to frosts. The forest on the south-eastern slopes are exposed to fewer hours of sun exposure, and are fed by moist air rolling in from the Indian Ocean, allowing the growth of the lush forests.

different measures of beta diversity (Koleff et al. 2003). By studying the processes and diversity patterns at ecotones we can additionally further our understanding of patterns and drivers of such changes.

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Michelle Greve

Department of Plant Science,
University of Pretoria, South Africa.

Email: michelle_greve@yahoo.com;

<http://www.up.ac.za/plant-science/article/44870/dr-michelle-m-greve>

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The less-splendid isolation of the South American continent

Only few biogeographic scenarios capture the imagination as much as the closure of the Isthmus of Panama. The establishment of this connection ended the “splendid isolation” of the South American continent (Simpson 1980), a continent that had been unconnected to any other land mass for over 50 million years. When the Isthmus rose out of the water some 3 million years ago (mya) the Great American Biotic Interchange started. Since terrestrial biotic interchange was no longer blocked by the Central American Seaway, (asymmetrical) invasion of taxa across this new land bridge transformed biodiversity in North as well as South America (Leigh et al. 2014). Or so the story goes.

A recent paper by Montes et al. (2015) casts further serious doubt on this scenario from a geological perspective. They show that a river system existed, originating in the volcanic arc of Panama and flowing into northern Colombia, about 15 to 13 mya. They base this hypothesis on geological mapping in conjunction with geochronological analyses of river deposits found in northern Colombia. With this they built on previous work (Farris et al. 2011, Montes et al. 2012a,b) in which the hypothesis of a fairly recent closure of the Isthmus was also questioned. Montes et al. (2015) reason that when a river system existed in the Panama-Colombia area, a terrestrial connection needed to be present. Any connection between the Caribbean Sea and Pacific Ocean could only have existed to the west of the current day Panama Canal area, where they postulate the origin of this river system.

So, how do these data fit in with what biologists know about migrations between North and South America? Leigh et al. (2014) provide a comprehensive overview of the historical biogeography of the Isthmus and review for instance that ground sloths had reached North from South America around 10 million years ago and Panama was well populated with all kinds of animals in the Early Miocene (18-19 mya), that fresh water fishes already dispersed in the late Miocene between

lower Central America (Costa Rica) and South America (northern Colombia), and that some snapping shrimp populations were already split long before the Isthmus had finally closed (most between 7–10 mya but some >15 mya). Next to this, several papers showed that plants also migrated between North and South America prior to the closure of the Isthmus (e.g., Erkens et al. 2007, Bacon et al. 2013), although for plants it is difficult to rule out that this happened via long-distance dispersal. Thus, the new findings of Montes and colleagues fit much better with a wealth of evidence from the biological realm that has been amassed over the last years, than the old model of a relatively rapid rise of the Isthmus.

If the land-bridge was available much earlier to many terrestrial organisms, the question that remains, of course, is why they only began to migrate in large numbers between North and South America around 3 mya? The generally accepted scenario that a wide seaway blocked their path is, given the above mentioned studies, not supported. The answer can probably be found in two directions. First of all, the sudden onset at 3 mya is just a remnant from past analyses. As discussed above, earlier migrations indeed have been found and the onset itself of the interchange is placed much earlier than previously accepted (Carrillo et al. 2015), starting already around 10 mya. Although the bulk of migrations might have happened more recently, the onset is more gradual than was postulated. Second, another type of explanation can be found in the type of vegetation present (Leigh et al. 2014), accepting that species ranges can be limited by more than geographic barriers alone (Feeley et al. 2014). Due to climatic cooling around 3 mya a corridor of grassland and savannah allowed open-country animals and some plants to move between North and South America (Molnar 2008, Bacon 2013). Before and after cooling such migration was not possible since tropical forests formed effective obstacles to any migration of these open-country animals. Support for such a scenario is, for instance, provided

by phylogenetic studies on birds of families that are restricted to tropical forests. They have been shown only to move from South to North America after formation of the land bridge and origination of tropical forests (Weir et al. 2009). Further phylogeographic studies in Central America might help to unravel the intricate connections between geology and biogeographic history in the region (e.g., Gutiérrez-García 2013).

To conclude, although the Isthmus might have reached its current shape for the first time around 2.7 mya (Late Pliocene; Molnar 2008), the formation of the land bridge and the onset of the Great American Biotic Interchange is pushed much further back in time than generally thought. This means that the “splendid isolation” of the South American continent is at least 10 million years shorter than originally postulated. This finding is highly relevant since an earlier rise of the Isthmus has profound implications for paleoclimatic modelling of sea currents. These models in their turn impact for instance biogeographic colonisation scenarios of the Caribbean islands and play a role in the understanding the onset of Plio-Pleistocene glaciations (Molnar 2008). Also, estimates of climate are influenced by this finding, determining the availability of suitable habitats for migration, again impacting biogeographic scenarios. Even the way the Andes has formed and our understanding of the wetland origin of the Amazon basin will be impacted by this new finding (Bacon et al. 2013, Hoorn and Flantua 2015). Montes et al. (2015) therefore have made a valuable geological contribution to the further unravelling and understanding of a major biogeographical event.

Roy Erkens

Maastricht Science Programme, Maastricht
University, The Netherlands
roy.erkens@maastrichtuniversity.nl
www.royerkens.nl

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Strong genetic structure among coral populations within a conservation priority region, the Bird's Head Seascape (Papua, Indonesia)

Craig J. Starger^{1,2,3}, Mark V. Erdmann⁴, Abdul Hamid A. Toha⁵, Andrew C. Baker⁶, and Paul H. Barber^{7*}

¹Department of Ecology, Evolution, and Environmental Biology, Columbia University, MC-5557, 1200 Amsterdam Avenue, New York, NY 10027 USA. ²Sackler Institute for Comparative Genomics, American Museum of Natural History, 79th Street and Central Park West, New York, NY 10024 USA. ³American Association for the Advancement of Science Washington, DC, 20005, USA. ⁴Conservation International, Indonesia Marine Program, Jl. Dr. Muwardi No. 17, Renon, Bali 80235 Indonesia. ⁵Fishery Department, State University of Papua. Jl. Gunung Salju Amban, Manokwari, Papua Barat, 98314, Indonesia. ⁶Department of Marine Biology and Ecology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149 USA. ⁷Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, 90095.

*corresponding author: paulbarber@ucla.edu

Abstract. Marine Protected Areas (MPAs) are widely considered to be one of the best strategies available for protecting species diversity and ecosystem processes in marine environments. While data on connectivity and genetic structure of marine populations are critical to designing appropriately sized and spaced networks of MPAs, such data are rarely available. This study examines genetic structure in reef-building corals from Papua and West Papua, Indonesia, one of the most biodiverse and least disturbed coral reef regions in the world. We focused on two common reef-building corals, *Pocillopora damicornis* (Linnaeus 1758) and *Seriatopora hystrix* (family: Pocilloporidae), from three regions under different management regimes: Teluk Cenderawasih, Raja Ampat, and southwest Papua. Analyses of molecular variance, assignment tests, and genetical bandwidth mapping based on microsatellite variation revealed significant genetic structure in both species, although there were no clear regional filters to gene flow among regions. Overall, *P. damicornis* populations were less structured ($F_{ST} = 0.139$, $p < 0.00001$) than *S. hystrix* ($F_{ST} = 0.357$, $p < 0.00001$). Despite occurring in one of the most pristine marine habitats in Indonesia, populations of both species showed evidence of recent declines. Furthermore, exclusion of individual populations from connectivity analyses resulted in marked increases in self-recruitment. Maintaining connectivity within and among regions of Eastern Indonesia will require coral conservation on the local scales and regional networks of MPAs.

Keywords. Coral Triangle, Marine Connectivity, Conservation, Papua, Bird's Head Seascape

Introduction

Comprising only a small fraction of the surface of the Earth's oceans, coral reefs are the world's most biologically diverse marine ecosystems (Connell 1978, Reaka-Kudla 1997). Despite the ecological and economic importance of coral reefs, they are rapidly declining worldwide due to anthropogenic stressors (Hoegh-Guldberg et al. 2007, Burke et al. 2012). On many reefs worldwide coral cover has declined by 50–80% over the last few decades (Gardner et al. 2003, Bruno & Selig 2007, De'ath et

al. 2012, Jackson et al. 2014). The loss of habitat-building reef corals compromises the very foundation of coral reef ecosystems (Adams and Ebersole 2010, Hughes et al. 2010), threatening marine biodiversity and the important economic goods and services that this diversity supports. In Southeast Asia, 95% of reefs are considered under threat and there is an urgent need for coral and coral reef-focused conservation (Burke et al. 2012).

Marine protected areas (MPAs) are considered one of the best methods for protecting spe-

cies diversity and ecosystem processes and functions (Levitan and McGovern 2005). As such, the Convention on Biodiversity (2006) set a goal that at least 10% of each of the world's marine and coastal ecoregions should be set aside as marine protected areas by 2020. Given that only ~3% of the world's marine ecosystems are currently within MPAs (Toropova et al. 2010, IUCN 2013¹), there should be significant growth in MPAs around the world, including coral reef ecosystems. Therefore, there is a pressing need for sound science to support marine conservation efforts. In particular, understanding connectivity, the exchange of dispersive larvae among populations that contributes to population demographics and gene flow, is critical to developing long-term conservation strategies for marine ecosystems (Crowder et al. 2000, Botsford et al. 2001, Palumbi 2003, Cowen et al. 2006). However, understanding patterns of connectivity remains among the most crucial gaps in scientific knowledge necessary for marine conservation (Sale et al. 2005).

The Coral Triangle (*sensu* Veron et al. 2009), a region that includes Malaysia, the Philippines, Indonesia, Timor Leste, Papua New Guinea, and the Solomon Islands, is the most biologically diverse marine ecosystem in the world (Roberts 2002, Bellwood and Meyer 2009); it is also among the most threatened (Burke et al. 2012). Coral diversity peaks in the provinces of Papua and West Papua, Indonesia (Veron et al. 2009), a region collectively referred to as the 'Bird's Head Seascape'. A multi-institutional program that includes NGOs, universities, and local governments, the Bird's Head Seascape Initiative is working to confront the threats to marine habitats in this region by designing and implementing an ecosystem-based management plan, including an interconnected network of MPAs (Mangubhai et al. 2012). Therefore, understanding patterns of genetic connectivity among populations of corals and reef-associated species within this region has become a key research priority for conservation practitioners.

While the presence of genetic connectivity does not ensure demographic connectivity, restricted genetic connectivity is a clear sign that

demographic connectivity is extremely limited or absent (Hedgecock et al. 2007). As such, studies have used genetic connectivity to advance marine conservation goals from a variety of perspectives (e.g. Palumbi 2003, Laurie et al. 2004, Kool et al. 2011, Berger et al 2014, DeBoer et al. 2014, Serrano et al. 2014, Treml et al. 2015). In one particularly novel approach, Baums et al. (2005) simulated how the loss of individual coral populations could impact regional patterns of genetic connectivity between Caribbean coral populations. This method is particularly useful in regions like West Papua, where rapid development requires informed decisions about which reefs should be prioritized for protection.

While phylogeography and genetic connectivity studies within the Coral Triangle have increased greatly in the past decade (see Carpenter et al. 2011 and Barber et al. 2011 for reviews), few of these studies focus on corals, highlighting a critical need for research on this foundational taxonomic group. Comparative population genetic studies on *Pocillopora damicornis* and *Seriatopora hystrix* (Ayre and Hughes 2000, 2004) along the Great Barrier Reef suggest that these two species are on opposite sides of the genetic connectivity spectrum; typically *S. hystrix* populations have higher levels of structure while *P. damicornis* populations have minimal or no subdivision over spatial scales of 700–1200 km, although the latter can have substantial genetic structure on the periphery of its range (Ayre and Hughes 2004, Combsch and Vollmer 2011). Thus, these species provide an ideal range of dispersal ability for examining connectivity throughout the Bird's Head Seascape, the epicenter of coral diversity and the center of these corals' geographic ranges (Veron et al 2009).

In this study, we examine the genetic structure of *Pocillopora damicornis* and *Seriatopora hystrix* to improve our understanding of connectivity of coral populations in the Bird's Head Seascape, and to help conservation practitioners develop effective management strategies for coral reefs in this region. Specifically, we test the hypothesis that populations of *P. damicornis* are more open with lower levels of genetic structure,

¹ http://www.iucn.org/news_homepage/events/impac3/?13912/World-nearing-3-of-ocean-protection, last accessed 8/29/2015

while *S. hystrix* populations are more structured, resulting from more limited dispersal. Further, because of significant loss of coral reef habitat in Indonesia (Burke et al. 2012), we examine diversity of microsatellite allele variation to test for declines in effective population size and examine how the loss of individual coral populations in the Bird's Head Seascape could impact connectivity across this region.

Methods

Site descriptions

The Bird's Head Seascape is one of the most pristine marine ecosystems in Indonesia (McKenna et al. 2002, Burke et al. 2012), but threats to this ecosystem are increasing from a variety of sources (Varkeya et al. 2010). We focus on three regions – Teluk Cenderawasih, Raja Ampat and Southwestern Papua (Table 1, Fig. 1) – that represent distinct 'coral ecoregions' (Veron et al. 2009) with relatively limited connectivity among them (Trembl et al. 2015). Located on the northwestern shores of the island of New Guinea (Fig. 1), Teluk Cenderawasih could serve as important larval sources for Raja Ampat due to the New Guinea

Coastal Current (Nof 1995, Morey et al. 1999). However, Trembl et al. (2015) suggests that physical oceanography restricts connectivity between Teluk Cenderawasih and Raja Ampat, a prediction supported by genetic isolation (Crandall et al. 2008, DeBoer et al. 2008, Nuryanto and Kochzius 2009, DeBoer et al. 2014, Jackson et al. 2014) and range restricted endemics (Wallace et al. 2011, Allen and Erdman 2012) within the bay. Although technically outside Teluk Cenderawasih, Lemon, Adoki and Owi islands lie within the 'Cenderawasih Bay' coral ecoregion (Veron et al. 2009) and cluster with Teluk Cenderawasih in the analyses of Trembl et al. (2015). Similarly, models by Trembl et al. (2015) indicate that Southwestern Papua, represented by the populations Fakfak and Kaimana, is also relatively isolated.

The 12 actively managed MPAs in the Bird's Head Seascape range in size from 5000 to 1,453,500 ha, covering a total area of 3,594,702 ha (see Mangubhai et al. 2012). Approximately 50% of Raja Ampat's reefs are included in a network of seven marine protected areas ranging in size from 34,000 ha to 343,200 ha and separated by 20–100 km (Varkeya et al. 2010). A single MPA

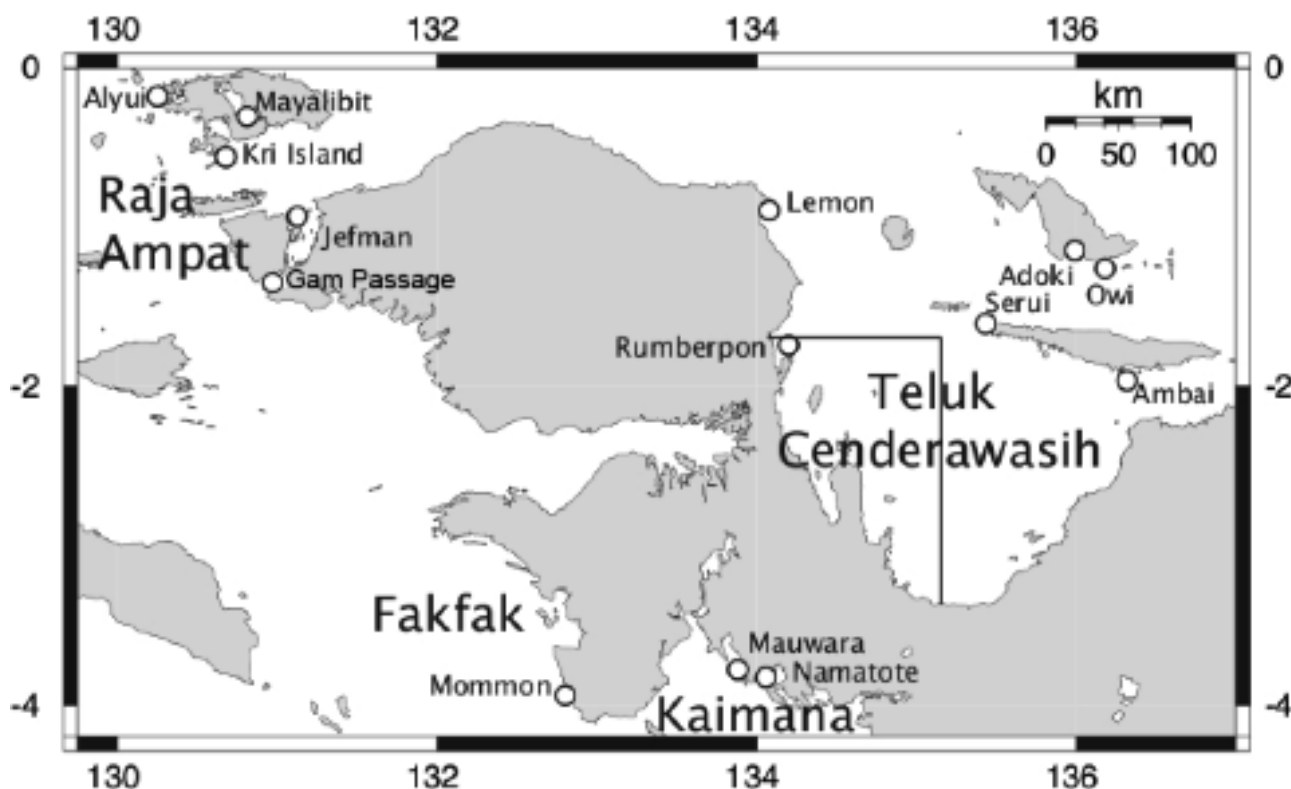


Figure 1. The Bird's Head region of West Papua, Indonesia. Sampling localities are shown as white circles. The solid black line delineates the border of Teluk Cenderawasih National Park.

Table 1. Sampling locations in Papua and West Papua, Indonesia

Region	Locality	Latitude	Longitude	Number of samples	
				<i>P. damicornis</i>	<i>S. hystrix</i>
Raja Ampat	Alyui Bay	0° 10.47 S	130° 14.85 E	20	19
	Mayalibit	0° 17.85 S	130° 48.49 E	9	20
	Kri Island	0° 33.38 S	130° 40.68 E	30	9
	Jefman	0° 55.64 S	131° 07.41 E	22	22
	Gam Passage	0° 25.88 S	130° 33.16 E	4	0
Teluk Cenderwasih	Lemon	0° 53.41 S	134° 04.90 E	18	20
	Rumberpon	1° 44.23 S	134° 12.15 E	13	19
	Adoki Village	1° 08.53 S	135° 59.68 E	10	12
	Serui	1° 54.32 S	136° 13.65 E	6	0
	Owi	1° 15.26 S	136° 10.99 E	9	9
	Ambai	1° 57.64 S	136° 19.23 E	15	22
Fakfak / Kaimana	Mommon	3° 56.38 S	132° 48.21 E	4	18
	Mauwara	3° 49.65 S	134° 03.51 E	23	0
	Namatote	3° 46.73 S	133° 52.93 E	0	21
	Total			169	191

of 1,453,500 ha covers 30% of Teluk Cenderawasih (The Taman Nasional Teluk Cenderawasih, or Cenderawasih Bay National Park, Fig. 1), and the Kaimana MPA covers all of Kaimana's jurisdictional waters (597,747 ha) (Mangubhai et al. 2012).

Genetic analysis

Field collection and microsatellite analysis of 14 *Pocillopora damicornis* and *Seriatopora hystrix* populations in the Bird's Head Seascape (Table 1) followed Starger et al. (2008). Hardy-Weinberg equilibrium and allelic diversity measures for these populations are available in Starger et al. (2010).

To test for genetic structure among sample locations, we analyzed data from each species with AMOVA (Excoffier et al. 1992) as implemented in Arlequin 3.5.1.2 (Excoffier and Lischer 2010). We first assumed no regional genetic structure among sample locations, then performed hierarchical AMOVA partitioning populations into Raja Ampat, Teluk Cenderawasih, and Southwestern Papua coral ecoregions (Veron et al. 2009). Signifi-

cance was tested with 20,000 random permutations using the infinite alleles model (IAM, represented by *F* statistics; Weir and Cockerham 1984) and the distance-based, stepwise mutation model of microsatellite evolution (SMM, represented by *R* statistics; Slatkin 1995). To prevent artifacts due to clonal reproduction, only unique genets (samples with non-identical genotypes) were included in the analyses.

To examine genetic structure without *a priori* assumptions, we employed spatial and non-spatial Bayesian assignment methods implemented in BAPS 5.3 (Corander and Marttinen 2006, Corander et al. 2008) as described by Starger et al. (2010). We also employed individual-based assignment tests implemented in Structure 2.2.2 (Pritchard et al. 2000, Falush et al. 2003, Hubisz et al. 2009) using the admixture model with no prior information on population origin. We performed 300,000 iterations, discarding the first 100,000 as burn-in. We tested *K* values from 2 to 15 and used the Delta *K* method (Evanno et al. 2005) to determine the most likely *K* value.

To further explore dispersal barriers, we

used 'genetical bandwidth mapping' as implemented in the GenbMap (Cercueil et al. 2007). This method identifies spatial discontinuities in allele frequencies that may represent barriers to dispersal, but unlike model-based approaches, this nonparametric method does not assume a particular measure of genetic distance. Genetical bandwidth mapping is particularly relevant to studies where fine-scale structure is stronger than regional structure, which can occur in low-dispersal species, and for studies with low and irregular sample sizes (Cercueil et al. 2007) as is common with corals in the hyper-diverse Coral Triangle. GenbMap was run with a resolution of 300 x 300 pixels (1 pixel = 2.1km), 200 iterations, and $p = 0.05$. Since GPS coordinates were only taken at each locality, each individual coral's GPS coordinates were randomly perturbed by 10 m following the example of Cercueil et al. (2007). Statistical significance of the resulting 'genetical regions' was tested using AMOVA.

To test for population declines in coral populations in this region, we calculated the statistic "M" following Garza and Williamson (2001). Briefly, M is the ratio of the number of alleles to range in allele size. Ratios of 0.8 and above are common for stable populations, but populations that have experienced reductions in effective population size have values below 0.70. As *P. damicornis* and *S. hystrix* are hermaphroditic (Veron 1986) and effective population size cannot be skewed by unequal sex ratio, fluctuations in effective population can only be driven by changes in actual population size.

Finally, we examined the functional loss of individual coral populations on regional connectivity by employing the jackknifing procedure of Baums et al. (2005). Briefly, we estimated pairwise immigration rates between populations with $n \geq 9$ using a Bayesian assignment method implemented in the program BayesAss+ 1.3 (Wilson and Rannala 2003) which estimates migration among all populations simultaneously. The first 999,999 iterations of the MCMC were discarded as burn-in. The chain was then run for an additional 2 million iterations with a sampling frequency of 2,000, allowing convergence of likelihood scores (data not

shown). Finally, we generated additional migration matrices for each species, but with a single locality removed, and then calculated the mean effect of removal of each locality on mean self-recruitment of the remaining sites by subtracting self-recruitment rates of the truncated matrices from the complete genetic connectivity matrix and averaging across localities.

Results

Allelic variation in microsatellites

We genotyped 169 individual *Pocillopora damicornis* (Table 1) at nine microsatellite loci. Number of alleles per locus ranged from seven (Pd3-005) to 20 (PV2) with a mean of 11.67 (Table 2). Five multilocus genotypes were observed in more than one individual, suggesting the possibility of clonality, and two of these were observed in more than two individuals. In total, nine clonal individuals were removed from the analysis. Similarly, we genotyped 191 individual *Seriatopora hystrix* (Table 1) at seven microsatellite loci. The number of alleles per locus ranged from three (Sh3-003) to 19 (Sh2-006) with a mean of 10.57 (Table 3). Six multilocus genotypes were observed in more than one individual, suggesting clonality, and one of these was observed in more than two individuals. These six potentially clonal individuals were removed from subsequent analyses. Details of Hardy-Weinberg equilibrium (HWE), linkage disequi-

Table 2. Population statistics for *Pocillopora damicornis*: Given are the number of samples (N), number of unique genotypes (Ng), M value (M), its variance (M var), and BAPS cluster.

Locality (region)	N	Ng	M	M var	Cluster
Alyui Bay (R4)	20	16	0.61	0.07	1
Mayalibit (R4)	9	9	0.63	0.07	2
Kri Island (R4)	30	30	0.61	0.06	2
Jefman (R4)	22	22	0.72	0.06	3
Lemon (TC)	18	18	0.64	0.08	4
Rumberpon (TC)	13	13	0.62	0.04	3
Adoki Village (TC)	10	7	0.61	0.07	2
Owi (TC)	9	9	0.67	0.08	3
Ambai (TC)	15	15	0.62	0.05	3
Mauwara (F/K)	23	21	0.59	0.05	5

Table 3. Population statistics for *Seriatopora hystrix*: Given are the number of samples (N), number of unique genotypes (Ng), *M* value (M), its variance (M var), and BAPS cluster.

Locality (region)	N	Ng	M	M var	Cluster
Alyui Bay (R4)	19	17	0.61	0.06	1
Mayalibit (R4)	20	20	0.49	0.09	2
Kri (R4)	9	9	0.62	0.03	1
Jefman (R4)	22	17	0.66	0.07	3
Lemon (TC)	20	20	0.67	0.09	4
Rumberpon (TC)	19	19	0.79	0.09	5
Adoki Village (TC)	12	12	0.7	0.11	6
Owi (TC)	9	9	0.79	0.09	7
Ambai (TC)	22	22	0.72	0.08	8
Mommon (F/K)	18	18	0.7	0.1	9
Namatote (F/K)	21	21	0.81	0.08	10

librium and tests for null alleles are reported in Starger et al 2010 and Supplemental Table 1. Briefly, no locus was consistently out of HWE in all localities, and patterns suggest genetic subdivision at the local scale, combined with admixture of populations (Underwood et al. 2007).

Population genetic structure

AMOVA analysis with no *a priori* assumptions indicated strong structure in both species with $F_{ST} = 0.139$ ($R_{ST} = 0.130$) for *P. damicornis* and $F_{ST} = 0.357$ ($R_{ST} = 0.246$) for *S. hystrix* ($p < 0.00001$ for all values), with 16-17% and 30-37% respectively of the variation due to differences among localities (Tables 4 and 5). Results from the hierarchical AMOVA (Tables 4 and 5), however, did not support differentiation among the three biogeographic regions (Fig. 1). This hypothesis explained 0% of the genetic variation in *P. damicornis* and only 6.84% of the variation in *S. hystrix* using the infinite alleles model ($F_{CT} = 0.068$, $p = 0.03$); results of the stepwise mutation model were not significant ($R_{CT} = 0.043$, $p = 0.18$). Instead, variation among populations within regions explained 86.84% of the variation in *P. damicornis* with $F_{ST} = 0.132$ ($p < 0.00001$) and 63.02% of the variation in *S. hystrix*, with $F_{ST} = 0.370$ ($p < 0.00001$). Similar results were achieved using the stepwise mutation model (Tables 4 and 5).

Table 4. Results from AMOVA for *Pocillopora damicornis*. Four genetic structures are tested. "All samples" indicates that there was no hierarchical structure imposed. '3 regions' tests the significance of a priori geographic structure among Teluk Cenderawasih, Raja Ampat, and Fakfak/Kaimana. Finally, the structures inferred by BAPS and genetical bandwidth mapping (GBM) are tested. Estimators are calculated based on both the infinite alleles model (*F* statistics) and stepwise mutation model (*R* statistics) of microsatellite evolution. Negative values are presented, but are effectively equal to zero.

	F statistic	p	% var	R statistic	p	% var
All samples						
Among localities	F_{ST}	0.139	<0.00001	13.940	R_{ST}	0.130 <0.00001 13.000
Within localities			86.060			87.000
3 regions						
Among groups	F_{CT}	-0.028	0.874	-2.830	R_{CT}	0.017 0.382 1.660
Among localities within regions	F_{SC}	0.156	<0.00001	15.990	R_{SC}	0.120 <0.00001 11.810
Within localities	F_{ST}	0.132	<0.00001	86.840	R_{ST}	0.135 <0.00001 86.540
Structure inferred by BAPS						
Among clusters	F_{CT}	0.140	0.003	14.000	R_{CT}	0.060 0.240 6.020
Among localities within clusters	F_{SC}	0.030	0.007	2.610	R_{SC}	0.079 0.013 7.460
Within localities	F_{ST}	0.166	<0.00001	83.400	R_{ST}	0.135 <0.00001 86.520
Structure inferred by GBM						
Among clusters	F_{CT}	-0.011	0.555	-1.070	R_{CT}	0.063 0.178 5.930
Among localities within clusters	F_{SC}	0.148	<0.00001	14.940	R_{SC}	0.076 0.007 7.160
Within localities	F_{ST}	0.139	<0.00001	86.130	R_{ST}	0.136 <0.00001 86.530

Table 5. Results from AMOVA for *Seriatopora hystrix*. Four genetic structures are tested. "All samples" indicates that there was no hierarchical structure imposed. '3 regions' tests the significance of a priori geographic structure among Teluk Cenderawasih, Raja Ampat, and Fakfak/Kaimana. Finally, the structures inferred by BAPS and genetical bandwidth mapping (GBM) are tested. Estimators are calculated based on both the infinite alleles model (*F* statistics) and stepwise mutation model (*R* statistics) of microsatellite evolution. Negative values are presented, but are effectively equal to zero.

	F statistic			R statistic			
		p	% var		p	% var	
All samples							
Among localities	F_{ST}	0.357	<0.00001	35.710	R_{ST}	0.246 <0.00001	24.560
Within localities			64.290			75.440	
3 regions							
Among groups	F_{CT}	0.068	0.034	6.840	R_{CT}	0.043 0.177	4.290
Among localities within regions	F_{SC}	0.324	<0.00001	30.140	R_{SC}	0.222 <0.00001	21.210
Within localities	F_{ST}	0.370	<0.00001	63.020	R_{ST}	0.255 <0.00001	74.510
Structure inferred by BAPS							
Among clusters	F_{CT}	0.325	0.016	32.530	R_{CT}	0.286 0.018	28.620
Among localities within clusters	F_{SC}	0.050	0.088	3.400	R_{SC}	-0.054 0.919	-3.830
Within localities	F_{ST}	0.359	<0.00001	64.070	R_{ST}	0.248 <0.00001	75.220
Structure inferred by GBM							
Among clusters	F_{CT}	0.142	0.006	14.170	R_{CT}	-0.031 0.566	-3.080
Among localities within clusters	F_{SC}	0.263	<0.00001	22.610	R_{SC}	0.270 <0.00001	27.370
Within localities	F_{ST}	0.368	<0.00001	63.220	R_{ST}	0.243 <0.00001	75.710

Results from BAPS identified five genetic clusters from 12 *P. damicornis* localities, two of which were excluded due to low sample size (Table 2, Fig. 2), and ten genetic clusters in 11 *S. hystrix* populations (Table 3, Fig. 3). Clusters containing multiple populations were generally, but not always, composed of geographically proximal localities. For example, *P. damicornis* Cluster 1 includes four sites in Raja Ampat; however Cluster 2 consists of sites from Raja Ampat and Teluk Cenderawasih. For *S. hystrix*, Cluster 1 contained adjacent sites Kri Island and Alyui in Raja Ampat. Spatial clustering results were identical to the non-spatial clustering for both species, with the exception of *P. damicornis* in which Kri Island was assigned to Cluster 1 in the spatial analysis and clustered alone in the non-spatial analysis (not shown). The log(likelihood) values in the non-spatial analysis and spatial analysis for *P. damicornis* (-3,701.47 versus -3,718.95) and *S. hystrix* (-2,892.18 versus -2,916.11) were extremely similar, indicating close

agreement between the two methods, although the non-spatial analysis was still the best model. While AMOVA results based on BAPS partitions indicate significant variation among groups explaining 6% and 28% of the variation among regions of *P. damicornis* and *S. hystrix* respectively, the majority of the variation was still observed within localities (Tables 4 and 5).

The 'correct' number of clusters recovered in Structure 2.2.2 was unclear. Delta K indicated $K = 2$ as the most likely value for *P. damicornis* and $K = 12$ for *S. hystrix*, but in both species likelihood increased asymptotically as K values increased towards and then beyond the number of sampled localities (not shown). Results for $K = 2$ for each species indicate multiple clusters in both Raja Ampat and Teluk Cenderawasih, while Kaimana and Fakfak were contained mostly in one cluster (Figs 2 and 3). As a heuristic, we also present $K = 6$ for *P. damicornis* and $K = 11$ for *S. hystrix*, the most likely number of clusters indicated by BAPS (Table

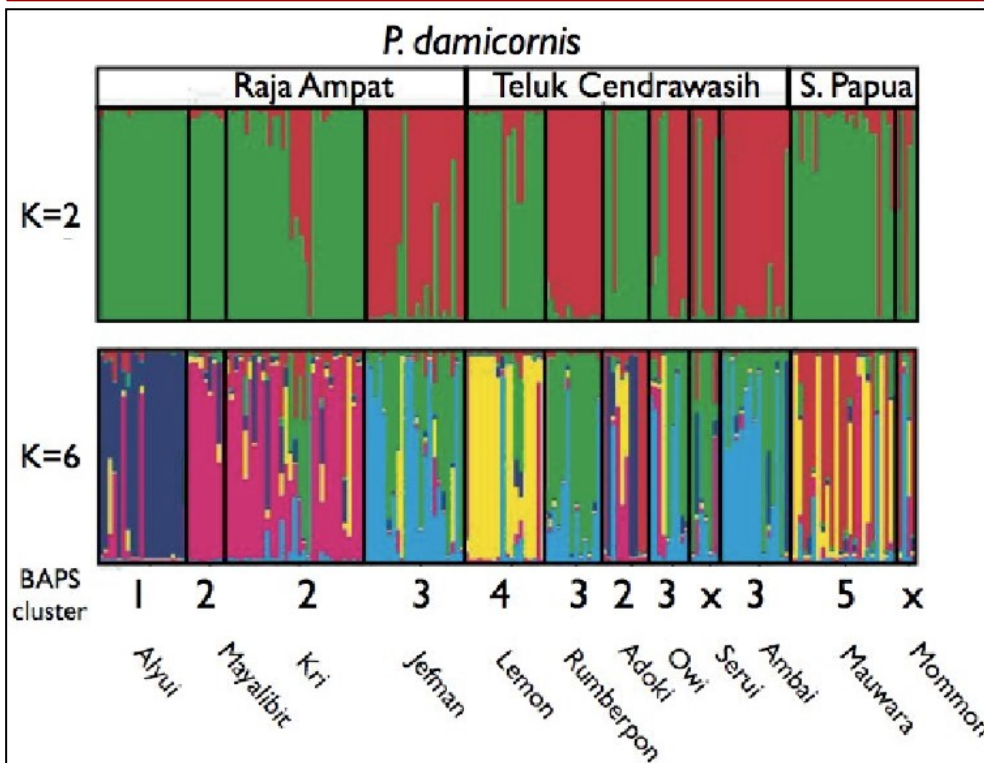


Figure 2. Results from Bayesian assignment methods implemented in Structure and BAPS for *Pocillopora damicornis*. X indicates populations excluded from BAPS analysis due to $N \leq 6$. Numbers of population clusters $K = 2$ and $K = 6$ were used to explore a range of cluster numbers as described in the text.

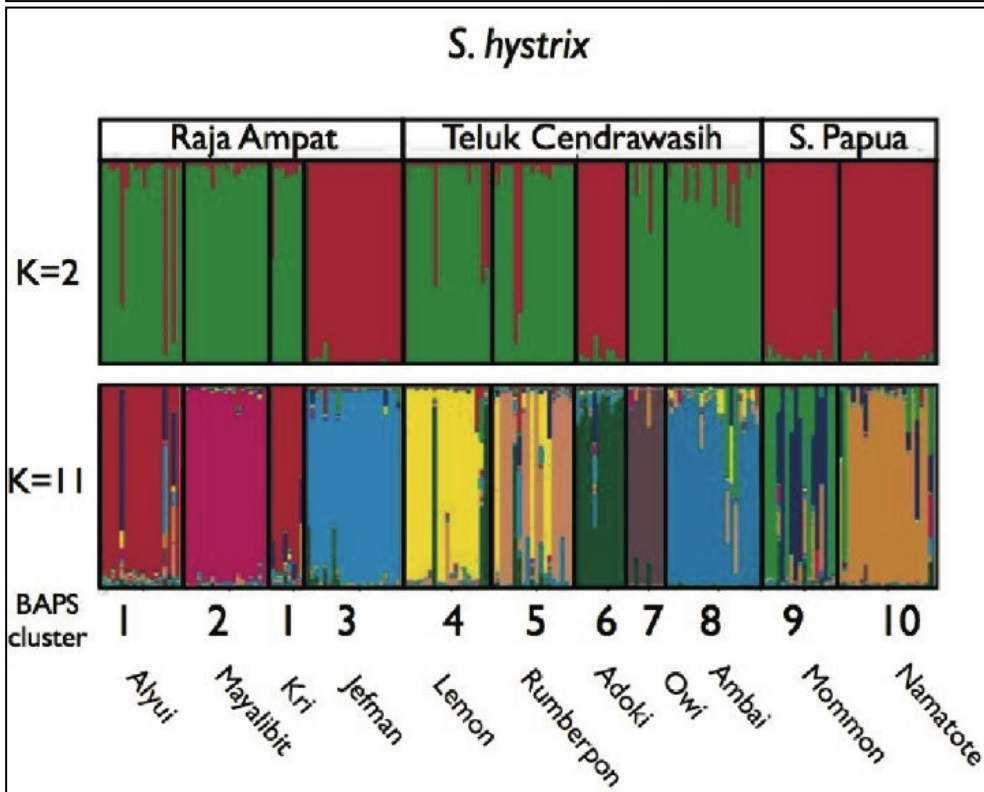


Figure 3. Results from Bayesian assignment methods implemented in Structure and BAPS for *Seriatopora hystrix*. $K = 2$ and $K = 11$ were used to explore a range of cluster numbers as described in the text.

2, Fig. 2). Results show a strong correspondence between cluster assignment and locality in *S. hystrix* (Fig. 3), whereas results from *P. damicornis* show less concordance between clusters and location (Fig. 2). In both species, admixture is evident because localities nearly always contain a mixed composition of individuals from various genetic clusters.

Genetical bandwidth mapping identified genetic discontinuities. At least six distinct 'genetical regions' were delineated for each species within the Bird's Head Seascape (Figs 4 and 5). Most notable are both a putative dispersal barrier between eastern and western localities within and above Teluk Cendrawasih, and genetic breaks in concordance with the land barrier

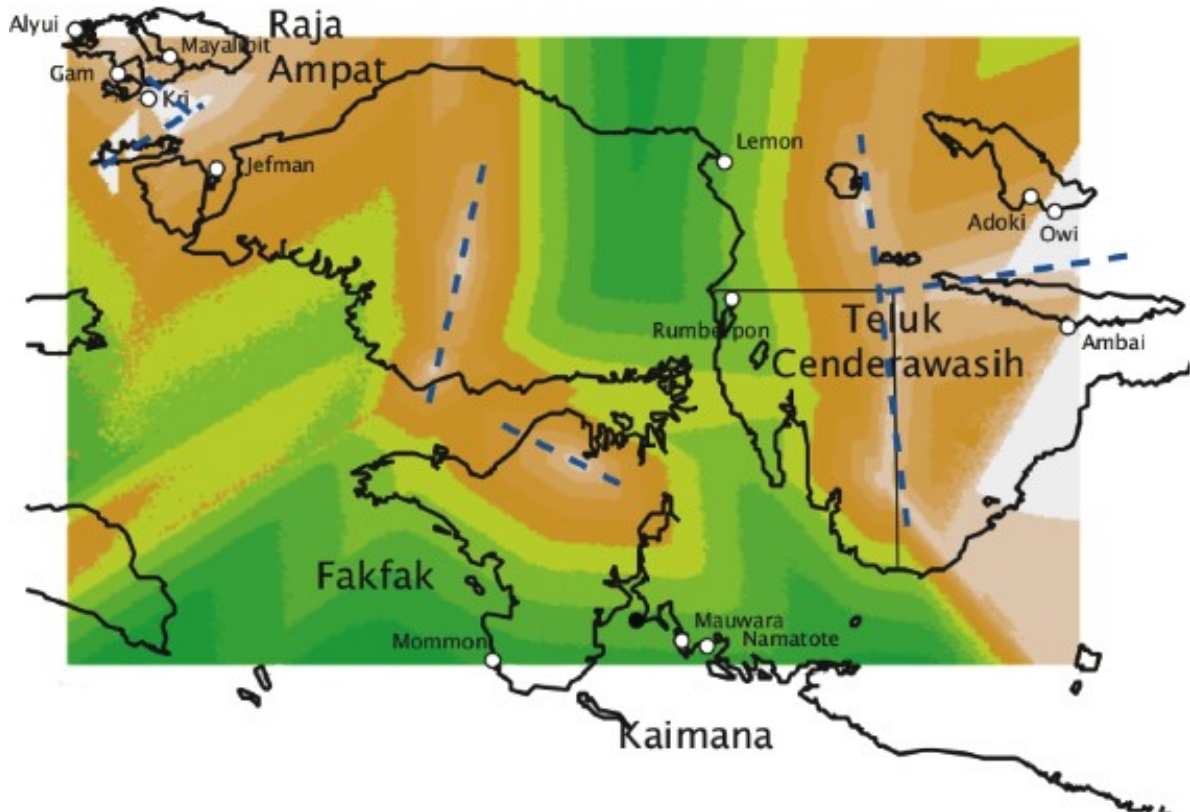


Figure 4. Genetical bandwidth map for *Pocillopora damicornis*. Green areas indicate regions of genetic homogeneity. White areas indicate putative barriers to larval dispersal and are highlighted with blue dashed lines. The solid black line indicates the borders of Taman Nasional Teluk Cenderawasih.

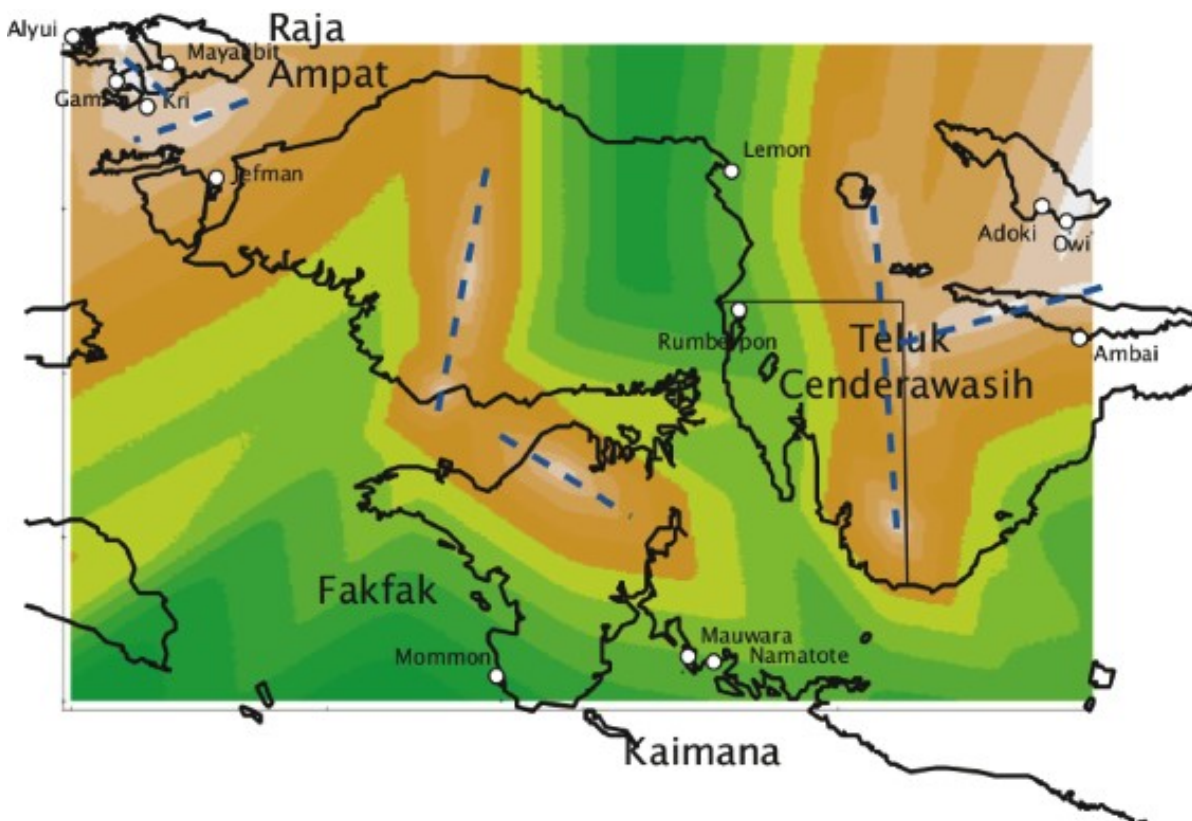


Figure 5. Genetical Bandwidth Map for *Seriatopora hystrix*. Green areas indicate regions of genetic homogeneity. White areas indicate putative barriers to larval dispersal and are highlighted with blue dashed lines. The solid black line indicates the borders of Taman Nasional Teluk Cenderawasih.

formed by the Bird's Head peninsula. The isolation of Mayalibit and Jefman from the other sites in Raja Ampat is also evident in both species, as is a genetic break between Adoki and Ambai, north of Teluk Cenderawasih. AMOVA based on the 'genetical regions' structure was only significant for *S. hystrix* when based on the infinite alleles model ($F_{CT} = 0.142$, $p = 0.006$ and Table 2).

Results from BayesAss+ showed high levels of self-recruitment. Results from BayesAss+ revealed an average self-recruitment rate of 76% (SD = 1%) for *P. damicornis* and 93% (SD = 1%) for *S. hystrix*. The removal of individual localities increased self-recruitment an average of 1.8% in the remaining localities for *P. damicornis* and an average of 2.6% in the remaining localities for *S. hystrix* (Fig. 6). The exclusion of *S. hystrix* in Rumberpon and *P. damicornis* in Adoki were the only instances in which self-recruitment decreased in the remaining localities.

Discussion

Microsatellite analyses using AMOVA, assignment tests, and genetical bandwidth mapping indicate significant genetic differentiation among *Pocillopora damicornis* and *Seriatopora hystrix* populations within the Bird's Head Seascape, Eastern Indonesia. Genetic structure was much stronger in *S. hystrix* than in *P. damicornis*, consistent with previous comparative studies from Eastern Australia (Ayre and Hughes 2000, 2004) and Indonesia (Starger et al. 2010). Levels of divergence in both species were substantially higher than observed over similar geographic ranges in the Great Barrier Reef (Ayre and Hughes 2000, 2004) and Western Australia (Underwood et al. 2007), and were much more similar to values seen in the extreme of these species' ranges (Ayre and Hughes 2004, Combsch and Vollmer 2011).

Strong, significant genetic structure in coral populations of West Papua indicates substantial limits to genetic and demographic connectivity (Hedgecock et al. 2007), yet there was no clear regional pattern to this structure. Although biophysical models predict limited connectivity among Teluk Cenderawasih, Raja Ampat, and Southwestern Papua (Trembl et al. 2015), AMOVA

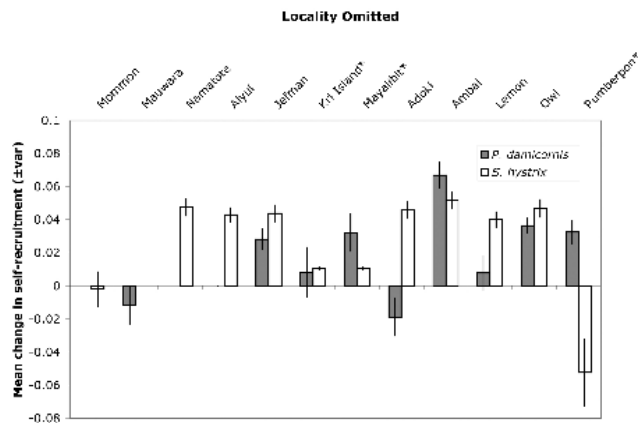


Figure 6. Jackknife analysis of self-recruitment rates depicting mean percent change in self-recruitment rates (\pm variance) among localities when one locality (labeled on the x-axis) is omitted. A negative value indicates a mean decrease in self-recruitment into the remaining localities when one locality is omitted. *Pocillopora damicornis* was not sampled in Mommon or Namatote. *Seriatopora hystrix* was not sampled in Mauwara. *indicates sites that lie within protected areas.

and assignment tests could not differentiate these three regions. The lack of clear regional genetic structure contrasts with results from a variety of other reef-dwelling invertebrate species that show pronounced genetic differentiation between Teluk Cenderawasih and other parts of the Bird's Head Seascape (Barber et al. 2006, Crandall et al. 2008, Barber et al. 2011, DeBoer et al. 2014).

Instead of regional structure, analyses revealed fine scale patterns of genetic structure within Teluk Cenderawasih and Raja Ampat. Lack of strong regional differentiation with pronounced genetic structure on the local scale was confirmed by genetical bandwidth mapping. This technique identified putative dispersal barriers within Raja Ampat and Teluk Cenderawasih, confirming that results from AMOVA and assignment tests are not artifacts of sample size. Mainland West Papua was also identified as a region of genetic discontinuity in both species (Figures 3 and 4), supporting the divergence of Teluk Cenderawasih and Raja Ampat as seen in a wide range of marine invertebrates in this part of the Bird's Head Seascape (Barber et al. 2011, Carpenter et al. 2011).

Differences between species

While both species exhibited significant genetic

structure across the Bird's Head Seascape, genetic structure was highest in *S. hystrix*. With the exception of Alyui with Kri Island, all other *S. hystrix* localities were genetically distinct. In contrast, *P. damicornis* populations exhibited much lower levels of genetic structure based on fixation indices, and clustering analyses, suggesting that this species has very different patterns of connectivity across the Bird's Head Seascape.

These differences in genetic structure may result from larval dispersal abilities. While the majority of larvae of both species have been observed to settle within a few days of release (Isomura and Nishihira 2001), maximum larval life spans may be higher than previously thought (Graham et al. 2010). In particular, *P. damicornis* larvae have survived 103 days in aquaria, indicating the potential for long distance dispersal (Richmond 1987). The presence of zooxanthellae in *S. hystrix* larvae coupled with evidence of diverse reproductive strategies such as polyp bailout (Sammarco 1982) and rafting (Jokiel 1984) suggests that extended larval durations may be possible in this species as well. However, the observation of higher structure in *S. hystrix* in comparison to *P. damicornis* in this and other studies (Ayre and Hughes 2000, 2004, Starger et al. 2010) suggests that *S. hystrix* must have lower larval dispersal abilities.

While our results are generally consistent with previous studies that compare genetic structure between these two coral species, we observed higher magnitudes of genetic structure over a smaller spatial scale in both species in the Bird's Head Seascape. Van Oppen et al. (2008) observed a mean pairwise F_{ST} of 0.20 among *S. hystrix* populations on the Great Barrier Reef, compared to $F_{ST} = 0.36$ across the Bird's Head Seascape, even though the spatial scale is considerably smaller. Physical oceanography, regional variation in reproduction, and more heterogeneous environmental conditions may explain the observed differences in connectivity among populations in these two coral reef ecosystems. For example, coral populations on the Great Barrier Reef are largely arranged in a linear pattern and are subjected to relatively predictable sea surface cir-

ulation patterns dominated by the Eastern Australian Current. Ocean circulation is much less well understood in the Bird's Head Seascape where coastlines are far more complex. This complexity may result in localized sea surface circulation eddies and seasonal or irregular reversals that could increase mean drift time between geographically proximate reefs.

An additional, non-mutually exclusive explanation is that there may be variations in reproductive strategies between corals of the Great Barrier Reef and those of the Bird's Head Seascape. It is well established that *P. damicornis* can be either a brooder or spawner depending on location (Baird et al. 2009) and may undergo 'reverse metamorphosis' from polyp to planula when stressed (Richmond 1985). In contrast, *S. hystrix* is not known to spawn, but can undergo polyp bailout when stressed (Sammarco 1982). It is therefore possible that regional differences in reproductive strategy between the Great Barrier Reef and the Bird's Head Seascape are contributing to the differences in observed genetic patterns. Similarly, *P. damicornis* has been observed rafting on pumice (Bryan et al. 2012), which could also facilitate higher dispersal and lower genetic structure in this species.

On coral species

An increasing number of studies indicate the presence of cryptic species in corals (e.g. Chen et al. 2007, Bongaerts et al. 2010, Souter 2010, Pinzon and LaJeunesse 2011). In particular, recent work by Pinzón et al. (2013) and Schmidt-Roach et al. (2013) indicate that *P. damicornis* is a species complex. Schmidt-Roach et al. (2013) identifies at least 5 cryptic lineages in the Western Pacific based on DNA sequences from the control region, internal transcribed spacer 2 (ITS2), and heat shock protein 70 and Combosch and Vollmer (*in press*) successfully differentiate ITS types 1, 3 and 5 based on based on 6,769 Single Nucleotide Polymorphisms (SNPs) obtained from RAD-Seq data.

While the above suggests that cryptic diversity within our samples likely impacts our results, particularly given that BAPS recovers 5 clusters, there are several reasons to believe that our re-

sults cannot simply be dismissed as the result of cryptic species diversity. First, Genetical Bandwidth Mapping recovers nearly identical patterns for both *P. damicornis* and *S. hystrix*. The most parsimonious explanation for this result is that the two species are being structured by similar physical processes (Avice 2000) rather than arising from concordant non-random distributions of cryptic lineages. In fact, while Bongaerts et al. (2010) suggest that there could be divergence among deep and shallow *S. hystrix*, their results suggest there is no cryptic divergence among shallow-water *S. hystrix* populations, such as those sampled in our study. Secondly, results show that populations generally fall into clusters based on geographic proximity. Given that many of the cryptic lineages can be distributed and genetically homogeneous over 1000s of km (Pinzón et al. 2013), it seems unlikely that multiple cryptic species in the Bird's Head Seascape would each dominate specific geographic regions. Lastly, results from Torda et al. (2013) on *P. damicornis* along the Great Barrier Reef are similar to previous research (e.g. Ayre and Hughes 2000, 2004) and show that the major genetic patterns are observed whether or not samples are segregated by cryptic lineage. As such, while cryptic lineages likely introduce noise into the *P. damicornis* results, it is unlikely that patterns of genetic structure are simply an artifact of taxonomic uncertainty.

Population decline and coral reef conservation

While the Bird's Head Seascape is relatively pristine (Mangubhai et al. 2012), our results suggest that corals may have suffered population declines in this region. *M* values averaged 0.64 for *P. damicornis* and 0.65 for *S. hystrix* with the majority of values falling below 0.70. These values are strikingly similar to those of the highly endangered Mediterranean Monk Seal ($M = 0.64$) and the Northern Elephant Seal ($M = 0.66$), two marine species that have suffered massive population declines (Garza and Williamson 2001), suggesting similar declines may have occurred in these two coral species. Increasing human pressures on coral reefs in the Bird's Head Seascape, coupled with increasing sea surface temperatures and episodes

of coral bleaching, are likely to exacerbate coral declines throughout the region unless conservation action is taken.

Marine conservation initiatives in coral reef regions are increasingly focused on designing and implementing effective networks of MPAs (Roberts 2005, Clifton 2009, Horigue et al. 2012, Mangubhai et al. 2012) with the optimal size and spacing of the individual MPAs within a network being a critical aspect of applied MPA research (Shanks 2003, Mills et al. 2010). While results indicate connectivity was largely limited among coral populations within the Bird's Head Seascape, results also indicated that MPA networks in this region could be impacted by the loss of individual populations. The jackknifing procedure of Baums et al (2005) showed that loss of individual populations raised mean self-recruitment rates in both species; in only 2 cases for each species did loss of a populations not impact self-recruitment.

Substantial increases in self-recruitment were seen in both species with the removal of Jefman, Ambai, and Owi, indicating that these locations are especially important for facilitating connectivity among populations in the Bird's Head Seascape. While it might be tempting to conclude that these populations are the most important to prioritize for conservation, designating a limited number of populations as strategically placed MPAs in hopes that they will seed adjacent unprotected areas would be an ineffective strategy to protect these coral populations. Likely, a more effective strategy would be a network that includes numerous, relatively closely spaced MPAs over a broad geographic area to provide protection of local reefs as well as support regional genetic connectivity. The network of seven MPAs in Raja Ampat is a good example of this approach, with an average MPA size of 160,000 ha and spacing averaging less than 60 km. However, further research is required to determine whether the number and spacing of these reserves is sufficient, and how many coral reef taxa will benefit from this arrangement. In contrast, the Taman Nasional Teluk Cenderawasih covers a large area, over 1 million hectares, but only includes the western half of the bay. Due to the genetic differentiation

of most local populations, it would be advisable to designate additional MPAs in the eastern north-east portions of the bay in the vicinity of Adoki and Owi to facilitate regional connectivity throughout Teluk Cenderawasih, as well as preserve the maximum amount of genetic diversity, protecting adaptive potential of these populations in the face of growing threats like climate change (Oliver et al. 2009) and ocean acidification (Pandolfi et al. 2011).

Increasing global and local threats to coral reefs is increasing the need for science to support conservation planning. Genetic investigations provide a disproportionately large amount of data relative to time spent in the field, and the results can help fill some of the most critical scientific gaps in understanding connectivity among MPAs (Sale et al. 2005). Although not all reefs can be assessed in this manner, insights into the patterns and processes of biological diversity can be used to design or refine management plans. In our case, the means to apply genetic data to conservation action already exists in the ongoing, multi-institutional partnerships of the Bird's Head Seascape Initiative (Green and Mous 2004). Examination of additional taxa in a similar fashion to that presented here (Barber et al. 2011, Carpenter et al. 2011) will provide a wide range of results that resource managers may take into account when designing an optimum MPA network for the Bird's Head Seascape and elsewhere.

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opinion

Bos primigenius in Ancient Egyptian art – historical evidence for the continuity of occurrence and ecology of an extinct key species

Carl Beierkuhnlein

Department of Biogeography, University of Bayreuth, Germany; carl.beierkuhnlein@uni-bayreuth.de

Abstract. Knowledge of the habitat requirements and temporal stability of populations of extinct aurochs (*Bos primigenius*) is surprisingly scarce. Reliable reports of this species, which by its domestication remains tremendously important for humans, are rare. As the species became extinct about 400 years ago and regionally disappeared much earlier, its behaviour and morphology are also under debate. Aurochs is a crucial component of the mega-herbivore theory in nature conservation, but in fact its natural habitat and behaviour are unknown. Here, I report records of aurochs for the time period of Ancient Egypt. They are found in archaeological sites and literature, and in collections. Records of the species continue through all the periods of Ancient Egypt. In particular, hunting scenes illustrating the merits of high-ranking persons, in their graves (mastabas) and temples, provide insights into the behaviour and ecology of the depicted game. Here, special attention is given to one outstanding hunting scene that is documented in a relief at the mortuary temple of Ramesses III (1175 BC, Medinet Habu, Egypt). Assisted by a group of hunters, the pharaoh kills three specimens of aurochs. The whole scene is stunningly realistic. The adult specimen is fleeing towards the reed belt of the River Nile, suggesting that the species' habitat was probably in large valley bottoms, where open grassland is regularly created by flooding. Endemic species of fish and game confirm that this scene took place in Lower Egypt. The regional populations of the North-African subspecies of aurochs probably went extinct shortly after this piece of art was produced. Records of species in ancient art can be very informative in terms of ecology and behaviour of species, especially when extinct species are addressed. In addition, the dating of old pieces of art containing biological information can be very precise, for instance when these refer to a historic personage.

Keywords. archaeozoology, aurochs, biodiversity loss, biogeography, extinction, hunting

Introduction: an iconic species

The motivation for this study is to bridge the gap between natural science and humanities in a field that is relevant for both sides. Pictures and artefacts in ancient cultures can be of high biological and ecological precision, they can be exactly dated, and they can be more abundant or frequent than remnants of organisms (e.g. bones). Traditional proxies for past environments and ecosystems such as pollen are preserved only under very specific conditions, refer to only few species, and dating precision can be low. Here, I focus on a key species of former ecosystems across the northern hemisphere, the aurochs, in order to improve the understanding of the ecology and biogeography of this important component of historical ecosystems. Besides woolly mammoth (*Mammuthus primigenius* Blumenbach 1799), aurochs (*Bos*

primigenius Bojanus 1827) is perhaps the most prominent extinct large herbivore in Europe, Northern Africa and Asia. Four centuries after its complete disappearance, this species is still vivid in tales and myths. Vernacular names exist in many languages (e.g. auerochs, auroch, ur, urus, bour, tur, tarva, reem) (van Vuure 2005).

The functional role of this species is currently under debate in European ecology and nature conservation (Birks 2005, Johnson 2009). It is seen as a lost key species. The occurrence of species that are dependent on open habitats, which applies for instance to a large proportion of the Central European flora, can only be understood if open gaps were created in densely wooded landscapes. Here, the impact of large herbivores on vegetation structure is discussed as one possibility (e.g. Vera 2000, Svenning 2002, Birks 2005, John-

son 2009). The mega-herbivore hypothesis in nature conservation is used as an argument to support the back breeding (towards aurochs; see below) of cattle that exhibit primordial traits. These animals are then utilized in the management of nature reserves.

Bos primigenius is the origin for domestic cattle (*Bos primigenius taurus* or *Bos taurus*). European cattle were probably derived from Near-Eastern populations of aurochs (Troy et al. 2001). However, early domestication, which began about 8000 years ago, took place independently in different regions, and also in North Africa (Loftus et al. 1994). Breeding was mainly directed towards transport, meat and milk production. Bone finds and historical sources indicate that remnant wild populations persisted for centuries in landscapes with domestic cattle (e.g. Lasota-Moskalewska and Kobryn 1990).

The body size of aurochs contributed both to its attraction and to its vulnerability. Skeletons indicate that aurochs were significantly larger than modern forms of cattle (Lasota-Moskalewska and Kobryn 1990). Even though less than 20 complete skeletons are known, it is clear that the north-eastern African populations of aurochs varied regionally in size (Linseele 2004).

The animal weighted approximately one tonne. The withers height (i.e. the height of the top of the shoulder blades) was 170 cm on average for males (maximum 200 cm) and 150 cm for female animals (van Vuure 2002). In contrast, domesticated cattle rarely reach 150 cm. Aurochs legs were longer than those of modern cattle, and the shape differed considerably, height of the aurochs' withers almost equalling the length of the whole body (Matolcsi 1970).

Paintings and pictures that show the colour of the fur and the animal's posture are prominent in Stone Age caves, especially in Spain and Southern France (e.g. Feruglio 2006). Then there is a gap in European figurative documents until Renaissance times, though the behaviour of the animal was still reflected in tales and myths. Several pictures, however, tend to reflect or exaggerate a romantic impression of the animal, and realistic scenes in natural settings are missing over millennia.

As was the case in Poland for the last 'wild' population of aurochs, it seems that as the aurochs became increasingly rare it was increasingly managed as game for the hunting privilege of the nobility (Guintard 1997). Possibly, such populations were kept in habitats that did not reflect the species' ecological niche. However, in Egypt this was not necessary because close to the banks of River Nile unmanaged floodplains always existed. There, it seems unlikely that bulls were kept and released to the wild just for hunting (Brewer et al. 1994).

Historical evidence of Aurochs distribution and regional climatic changes within the range of the species

Because of the importance of aurochs (as ancestor of cattle) and its assumed relevance as an ecosystem engineer for nature conservation and forestry, various attempts to back-cross primordial forms of *Bos primigenius* have been and still are undertaken (Heck 1951). Bone finds are the main form of evidence used to compare between the original and the bred forms of cattle with original characteristics. Realistic pictures of the species are rare in mediaeval European art. A famous mediaeval painting from Augsburg (Nehring 1898) that is copied in zoological textbooks is probably lost (van Vuure 2005). Other mediaeval and renaissance depictions are rare and of low precision (see also Pyle 1994).

Stone Age cave paintings of aurochs (and other species) represent the dawn of art and civilisation, with most prominent examples in the SE European caves Chauvet (32,000 years ago), Altamira (18,000 to 13,000 years ago) and Lascaux (17,000 to 10,000 years ago). The abundance of such *Bos primigenius* pictures indicates its outstanding importance both as game and as a threat for the human societies of the time. After the Neolithic period, there appears to be a gap in aurochs artefacts until the 16th century (van Vuure 2002).

Bos primigenius is known to have occurred in North Africa since the early Middle Pleistocene (Martinez-Navarro et al. 2014) and is from then on continuously documented until the late Pleisto-

cene (Churcher 1972, Uerpmann 1987, Gautier 1988, Kowalski and Rzebik-Kowalska 1991) and during the Holocene (Faith 2014). The most southern Pleistocene bone finds range as far south as Kashm el Girba in eastern Sudan, close to Eritrea (14°51' N, 33°25' E), and Erg Tihodaine in the Ahaggar Mountains, which is today in the centre of the Sahara (approx. 25°12' N, 6°30' E; map in Linseele 2004). During the Holocene, bone finds of aurochs range from the Nile delta down to Elephantine, which is 200 km south of Thebes (Linseele 2004). Many of the finds are not precisely dated.

With the sudden onset of humid conditions around 8500 BC, which was caused by a specific planetary constellation, currently hyper-arid desert was replaced by savannah vegetation (Ritchie and Haynes 1987). In this period, the Indian Ocean monsoon brought much more precipitation to NE Africa and floods of river Nile were much more intense (Maley 1977, Preusser 2009, Pross et al. 2009). Gradual aridification began 7300 years ago (Jung et al. 2004). Palynological data show the ecosystem transition over a period of about 2000 years (Kröpelin et al. 2008).

The expansion of the desert forced people to leave the degrading savannahs and establish settlements in the moist valleys, which was the start of advanced civilization (Kuper and Kröpelin 2006). The declining water levels of river Nile are well documented from the 1st up to the 5th Dynasty (until 2400 BC) (Pachur and Altmann 2006), which means that climatic changes continued during the early periods of Ancient Egypt.

Dobson (1998) suggests that native populations of aurochs in North Africa might have become extinct after the mid-Holocene. However, the high number of Holocene bone finds, reports, and especially the documented pieces of art in this study confirm the presence of the species until approximately 1000 BC. In agricultural literature, in archaeology, and in art, the appearance of the species in Egypt is cursorily pointed out (Hilzheimer 1917, Wildung, 2011). Aurochs populations must have been relatively large up to the Egyptian New Kingdom (1550–1050 BC), but it is very likely that hunting was reserved for the phar-

aoh. Hieroglyphs report that Amenhotep III (who reigned 1388–1351 BC) killed 96 animals (Strouhal 1989). It is unclear exactly when the species became locally extinct; van Vuure (2005) doubts whether the reported aurochs hunts of Ramesses II (1197–1165 BC) still took place at the River Nile.

In the Middle East, aurochs is documented in several Mesopotamian sources such as the epic of Gilgamesh (approx. 3000 BC) (van Vuure 2005). The aurochs population in Mesopotamia appears to have been very large, and its hunting is known in the cases of Assurnassirpal II (883–859 BC) and Sennacherib (704–681 BC) (van Vuure 2005).

In the Southern Levant, aurochs became probably extinct at the end of the Iron Age (records up to 500 BC) (Tsahar et al. 2009). Human population density increased strongly during this period, concentrated especially in the valleys that provided water for irrigation and substrate for agriculture. If the species was bound to wetlands and valleys, there would have been a conflict with human land use. Even so, it is very likely that hunting of the remnant populations was the final cause of aurochs.

The species was part of the late-glacial overkill, and was definitely erased from large parts of its Pleistocene distribution during the Greek and Roman civilisations. In his book on zoology, Aristotle lists the European bison (*Bison bonasus*) but does not explicitly mention the aurochs (cf. Balme 2002). He would not have ignored such an important species. At his time the species might have been extinct in Greece and Turkey, but the original zoological writings of Aristotle do not exist and what we know comes only from Arabian translations of them.

During Roman times, sporadic notes on aurochs in the Mediterranean exist, for instance by Julius Caesar, Seneca and Pliny the Elder (Pyle 1994). Presumably, some of these may relate to animals that were imported for performances in Roman arenas (Gautier 1988). It is unclear which aurochs populations were used for these shows, but it is unlikely that specimens were caught in remote Eastern European forests. Roman mosaics in Leptis Magna in Libya also show aurochs hunts or fights, but this does not necessarily confirm

remnant local populations. Leptis Magna was an important trading place for exotic wild animals for Roman circus games from the 1st to the 4th century AD (Bianchi Bandinelli et al. 1966). Further, without clear attribution to locations, the species is mentioned in the Bible under the Hebrew word for aurochs, “reem” (e.g. Books of Moses, Job and Isaiah). There, it is clearly stated that these bulls could not be tamed or used in agriculture.

In less developed continental Europe, aurochs populations could persist in the enormous forests. Mediaeval reports say that aurochs fought furiously when being hunted and trapped. The hot-tempered animal was very dangerous, especially when injured (van Vuure 2002). The rarer the species became, the more it was an exclusive privilege of the nobility to hunt this outstanding game. Aurochs had special status in the hunting rights of the European nobility (Wrzesniowski 1878, van Vuure 2002). The last remaining population was recorded in a large royal hunting reserve in Poland (Jaktórow Forest), including estimated numbers of individuals, until the early 17th century (Heymanowski 1972, van Vuure 2002). The last specimen died of natural causes during the chaos of the Thirty Years’ War, in 1627 AD. The population had not been protected and managed any more and had presumably declined below its viable population size.

Continuity of *Bos primigenius* in Ancient Egypt

During the early Holocene, aurochs was abundant across the Holarctic realm in Europe, Northern Africa and Asia ranging from the coast of the Atlantic Ocean to Korea (van Vuure 2002, Pushkina 2007). Subarctic regions and high mountains were not part of the species’ habitat.

Three subspecies of aurochs are differentiated in the literature: *Bos primigenius* ssp. *primigenius* (Bojanus 1827), *Bos primigenius* ssp. *namadicus* (Falconer 1859) and *Bos primigenius* ssp. *mauretanicus* (Thomas 1881, syn.: *B. primigenius africanus*, *B. primigenius ophistonomus*).

England was reached because large parts of the North Sea were terrestrial surface during the last glaciation period, with sea level about 120 m below current. Hall (2008) supports the hypothe-

sis, for the geographical distribution of post-glacial finds of aurochs in England, that the species was bound to low-lying flat sites such as broad valleys, which are exposed to floods and were unattractive for human settlements. Nevertheless, these sites are fertile and produce large amounts of biomass.

Knowledge of the occurrence of aurochs along the River Nile is based on bone finds (see also Gautier 1988, Linseele 2004) as well as historic references (Boessneck 1988, Yeakel et al. 2014). Archaeological records exist from the Pleistocene through Stone Age periods up to the rise of advanced cultures in Ancient Egypt.

In this study, additional aurochs records are documented (Table 1, Appendix). We can distinguish between hunting scenes in the wild, single depictions of the species in artefacts and scenes in captivity. Pictures of aurochs can be clearly distinguished from scenes with domesticated cattle. Cattle differ from aurochs in shape (and colour), but importantly cattle are mainly shown in an agricultural context, for instance pulling ploughs.

The documented pictures and artefacts show that aurochs was continuously present along river Nile over millennia. Wild aurochs existed during all flourishing periods of Ancient Egypt (Fig. 1). The phases of low numbers of records are the intermediate periods between the Old, Middle and New Kingdoms, where historical evidence is generally low.

The ecological content of the hunting scene in Medinet Habu

Hunting was an important activity of the upper class in Ancient Egypt. In order to continue hunting in the afterlife, realistic hunting scene paintings and reliefs were put for example in tombs and mortuary temples. Hunting of bovines was common (Manlius 2000) and aurochs was the only bovine game. Neither European bison (*Bison bonasus*) nor water buffalo (*Bubalus arnee*) occurred in Egypt and African buffalo (*Syncerus caffer*) was recorded only during the Pleistocene and moist periods of the mid Holocene (Yeakel et al 2014).

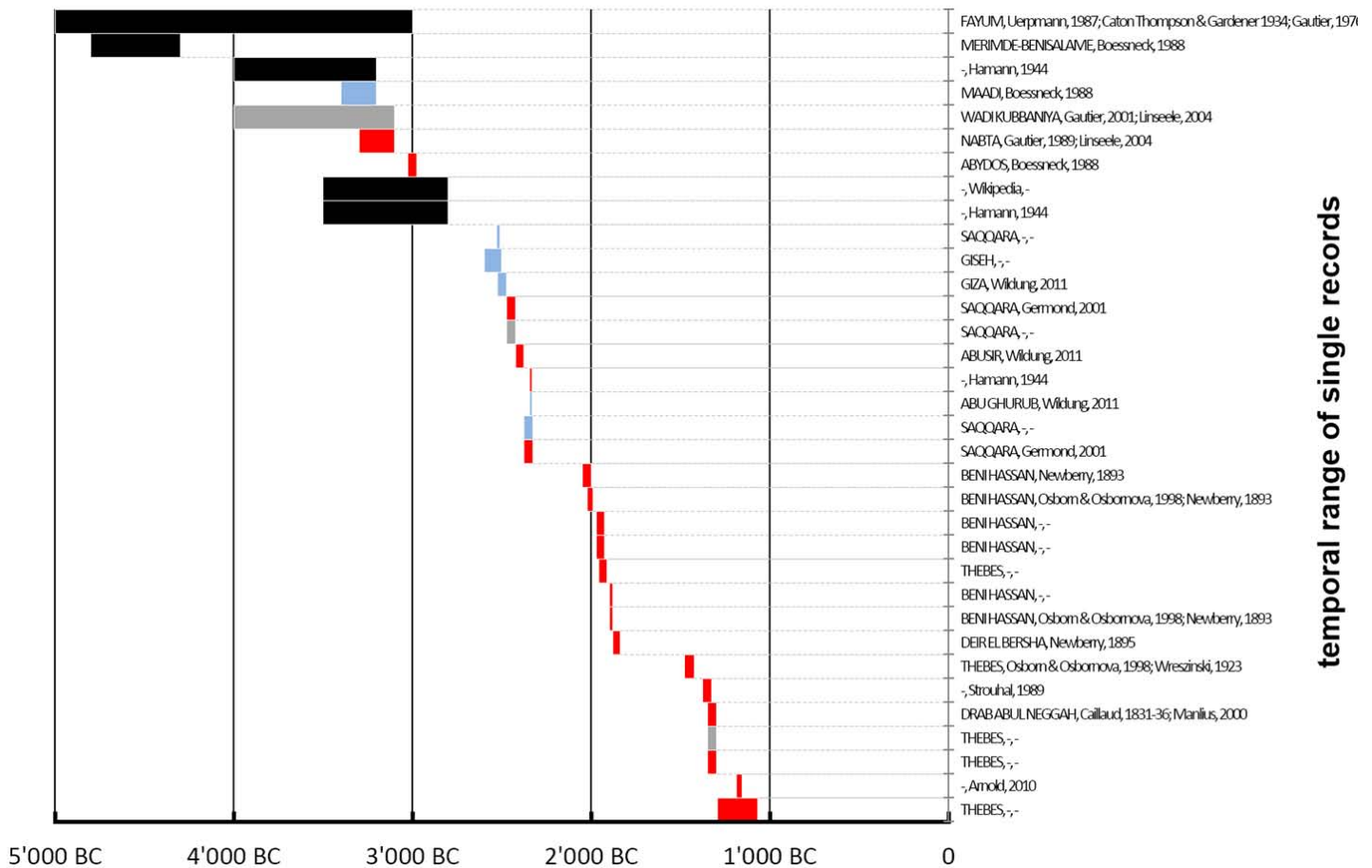


Figure 1. Records of *Bos primigenius* in Ancient Egyptian Art (n=34). Black – bone finds; red – hunting scenes in the wild; blue – animals held in captivity; grey – other artefacts (e.g. sculptures) and pictures. Records continue through all periods but are clumped in the Old, Middle and New Kingdom. Politically chaotic transition phases in between are poor in artefacts. All single records are documented in the electronic appendix (Table 1). Dating uncertainty is shown by the lengths of bars.

Several hunting scenes exist, where aurochs is shown together with ibex (*Capra nubiana*), antelopes (e.g. *Oryx dammah*, *Oryx leucoryx*, *Alcelaphus buselaphus buselaphus*, *Addax nasomaculatus*) and gazelles (*Gazella dorcas dorcas*, *Nanger soemmerringii*). Some of these species or subspecies are also regionally extinct. However, many scenes represent sequential arrangements of hunted species and not realistic impressions of animal communities in natural ecosystems. The scene in Medinet Habu is thus extraordinary (see next paragraph), and reflects the development of ecological knowledge (and art) in Ancient Egypt.

The mortuary temple of Ramesses III (Medinet Habu, Luxor) was completed in 1175 BC, during the life time of the pharaoh (who reigned 1186– 1155 BC) (Murnane 1980). On the south-western outer wall of this temple there is a stunning example of Ancient Egyptian art, which was

made to highlight the successes and achievements of the pharaoh. The hunting scene at the mortuary temple of Ramesses III demonstrates that aurochs lived at his time on the banks of river Nile (Fig. 2). In this period, aurochs hunting may have been reserved for the pharaoh and perhaps this scene shows one of the last hunts of all. In the scene, the large male aurochs is trying to escape towards the river. It has reached the dense reed-bed but there is no chance of escape. The injured bull is cornered by the hunters and its legs are collapsing in its struggle to reach the water.

The hunted animals are depicted with high morphological precision. These bovines clearly differ from domestic cattle. It is not only the shape of the horn, which cannot be taken as proof of wild aurochs because among the breeds of cattle in Ancient Egypt a huge variety of horn-shapes existed. As explained above, compared to domes-



Figure 2. The pharaoh Ramesses III is hunting aurochs on a chariot at the bank of the Nile. He is accompanied by bowmen and armed hunters. A large aurochs is hit by a spear and collapses in the dense reeds at the river margin with its tongue hanging out. Additionally, two juveniles are lying on the ground, one apparently dead with eyes closed and the other one bending its neck up. This relief is located on the back side of the large pylon in the temple of Medinet Habu (Thebes). The whole size of the scene (including Fig. 3 and 4) is approx. 9 x 9 m. The scene was not visible to the public but directed towards the private ritual palace of Ramesses III within the temple area. Photo C. Beierkuhnlein.

tic cattle, the legs of aurochs were long. The whole animal was very tall but Egyptian reliefs do not follow a standard scale. More importantly, it is discernible in the shape of the animal in this relief that the height of the withers almost equals the length of the body – again characteristic of aurochs (Matolcsi 1970; see above).

In pieces of Ancient Egyptian art, domestic cattle are always shown in a schematic way: as a donation to act as food supply for a dead person, in slaughtering scenes or being held on ropes. Hunting scenes, in contrast, are frequent in tombs (mastabas) and mortuary temples, and they always show animals in the wild.

Certainly, hunting domesticated cattle would not be of great honour for a pharaoh. After the regional extinction of elephants in North Afri-

ca, aurochs was the most dangerous game. No artist would have been assigned to illustrate a “cow hunt” in such an elaborate way, at such a special and prominent place as on the walls of the mortuary temple of Ramesses III. The location of the relief (which is several meters in breadth) at the back side of the large pylon, is of importance. On the other side of the pylon, facing to the visitors of the temple, the greatest military successes of the pharaoh are documented in scenes where he kills men from other countries. The hunting scene is equally large, but it was to be seen only from the private ritual palace of the pharaoh, and from his temple. Between the chariot and the hunted bull, a calf has fallen down and is lying on its back, with its neck upright. In the upper part of this scene another specimen has already been



Figure 3. Animals of the Nile River shown on the relief can be attributed to certain species of fish (centre on top: *Marcusenius cyprinoides*; upper right side: *Eutropicus niloticus*; bottom centre: *Alestes baremose*; centre and left lower margin: *Oreochromis niloticus*) and geese (cf. *Anser anser*). Photo C. Beierkuhnlein.

killed. The pharaoh himself is the one who kills the animals, though he is supported by a large group of hunters, lined up below the scene.

Various other species can be identified in this fascinating relief. Most notable is the thicket of reed (*Phragmites australis*) into which the aurochs is trying to flee. This vegetation is still characteristic of the margins of the Nile, today. It indicates the ambition of the artists to show the real habitat of the animal. In the water on the right-hand side, several species of fish can be identified, such as Nile Tilapia (*Oreochromis niloticus* syn. *Tilapia nilotica*) and others (cf. *Marcusenius cyprinoides*, *Eutropicus niloticus*, *Alestes baremose*) (Fig. 3). Geese (probably *Anser anser*) feed close to the water or fly away, upset by the hunt. At the top of the relief, more groups of game species can be seen (Fig. 4). *Equus* and *Oryx* are not proof of a location in Northeast Africa, but *Alcelaphus buselaphus buselaphus* was native to North Africa

(Holloway 1976) and did not occur in Mesopotamia or Asia. Locating the other mammal herds above the aurochs hunt may indicate a higher location, at the margin of the valley. In the narrow valley of the Nile, wetlands and mountainous habitats are found in close proximity, unlike in Mesopotamia.

This scene is a reflection of a local ecosystem. Together, the endemic fish and mammal species confirm that the depicted scene took place in Egypt. In the biological literature on aurochs, this relief (which is difficult to find, at the rear of the pylon) has hitherto been unknown (van Vuure 2005) or misinterpreted. Osborn and Osbornova (1998) reproduced a copy of an old photo (source Louis Grivetti) of this scene but erroneously assumed that the hunt took place in Mesopotamia. Indeed, following the construction of the Temple in Medinet Habu (1175 BC) there is no further evidence for the existence of aurochs in Egypt.



Figure 4. In the same relief at Medinet Habu, several herds of other herbivores are shown (*Oryx dammah* or *leucoryx*, *Equus africanus*, *Alcelaphus buselaphus buselaphus*). The lioness, which is attacking a wild donkey, indicates that this scene did not take place in captivity. Photo C. Beierkuhnlein.

There appears to have been a change in hunting practice over time. In the scene at Medinet Habu, two juvenile animals are killed. Older scenes of ‘hunting in the desert’ only show the killing of adult bulls, whereas cows and juvenile animals were allowed to escape (Manlius 2000) (Fig. 5). In the Egyptological context, ‘desert’ refers to natural ecosystems outside the agricultural landscape and settlements. Like in Mesopotamia, the hunting of aurochs was carried out with horse-drawn chariots, arrows and spears, sometimes supported by dogs. Hunting with horses is impressively portrayed on Tutankhamun's hunting chest lid (Sandison 1997).

Van Vuure (2002) argues that sedge marshes may have been the major habitat of *Bos primigenius*. As a large mammal that depended on local resources and did not migrate within its individual life cycle over large distances following seasonal availability of biomass, aurochs is not likely to have built up very large populations. Based on its

tooth structures, and on rare verbal descriptions, aurochs probably fed mainly on grasses and herbs (van Vuure 2002). This indicates that the species could hardly exist in closed-canopy forest with low biomass in the herb layer; it was more related to open gaps, grasslands, marshes and reeds. In forested landscapes with dense forests and closed canopies, such habitats depend largely on disturbances such as fire, wind throw or flooding.

Discussion

Regarding the scarcity of records, it comes as no surprise that knowledge of population trends, distribution, morphology and behaviour of aurochs is scarce. Even though pictures of aurochs are prominent in Stone Age caves, especially in Spain and France, there is an almost complete gap in figurative documents until Renaissance times, when only few low quality pictures were produced when the species was on the brink of extinction. Realistic scenes in nature are missing. Memory of the



Figure 5. Hunting scene in the tomb of Antefoker (1958–1913 BC) in Thebes (tomb number TT60) from the beginning of the 12th dynasty. In the second row, a male aurochs is hit by a spear and attacked by a hunting dog. The female animal (turning her head back) and the calf are allowed to escape. Species in this scene include: *Alcelaphus buselaphus buselaphus*, *Dama dama mesopotamica*, *Bos primigenius*, *Oryx leucoryx*, *Gazella dorcas dorcas*, *Vulpes vulpes*, *Lepus capensis*, and *Ammotragus lervia*. Photo Osiris Net.

species has mainly been passed on in tales and myths (van Vuure 2002).

The Egyptian culture did not produce natural science literature like the Greek culture did some centuries later. However, artists that decorated buildings such as the tombs and mortuary temples of important personalities had precise perceptions of nature. Until recently, this important source of biogeographical information has been ignored (Yeakel et al. 2014), though pitfalls

must be considered (Evans 2015). In this paper I have started to plug this gap, documenting what seems to be a continuous aurochs population alongside the Nile during the Holocene until approximately 1000 BC. These historical archives, most importantly the hunting scenes, have specific advantages and problems. Precision in the dating of these artefacts and pictures is extremely high. In addition, such scenes can include ecological information on the species' habitat. This makes

them superior to most other historical records.

Dating is best when the pieces of art are closely associated with the life of an individual person. Tombs were constructed during the lifetimes of pharaohs or high-ranking civil servants and not typically in the year of death. Nevertheless, this still gives a dating precision that is much higher than for radiocarbon dating. However, not all finds are clearly attributed to a person with a well-known lifespan. Additionally, the production of art is subject to political stability and economic prosperity. In times of chaos, as in the intermediate periods between the Old, Middle and New Kingdoms, evidence is lacking. As a result, the abundance of records is temporally patchy (see also Evans 2015).

Some pieces of Egyptian art are of astounding precision regarding animal morphology. In the Neferhotep tomb hunting scene, aurochs shows the characteristic whitish eel stripe on its back (Manlius 2000). Here, bull and cow are considerably different in size, which confirms the sexual dimorphism of the few complete skeletons. In the scene at Medinet Habu, we can see the reed belt of the River Nile. Such places close to the river were highly dynamic and fluctuating in extent because of seasonal flooding, erosion and sedimentation. The image at Medinet Habu is very likely to depict the characteristic natural habitat of the species. If so, aurochs may not have created open forest gaps for herbs and grasses as the mega-herbivore theory assumes (Birks 2005). It is known from other regions that the preferred habitats of aurochs were dense forests on valley bottoms, wetlands and river banks (Hall 2008, Tsahar et al. 2009). Aurochs may still have acted as an ecological engineer and key species in Ancient Egypt. However, open space with grassy vegetation was probably created not by the animal itself but rather by the flooding regime of a braided river.

It is generally assumed that southern habitats served as refugia during the LGM for species such as aurochs (Sommer and Nadachowski 2006). Nevertheless, there is evidence that the Holocene warming did not lead to substantial population growth in aurochs (Mona et al. 2010), which could be a result of human hunting pressure. In north-

ern Africa, during the Pleistocene, arid conditions and sand dune formation coincided with intense Arctic glaciation and low sea levels, resulting in a high degree of connectivity between Africa and Asia because neither the Persian Gulf nor the Red Sea functioned as marine barriers (Williams 2009). The Holocene then brought drastic changes in precipitation regimes. Desert climate was replaced by humid conditions between 8500 BC and 3500 BC (Preusser 2009). The maximum monsoon rainfall occurred around 6500 BC, when lakes and wetlands were common in the present-day Sahara (Pachur and Altmann 2006). The zonal vegetation was characterized by savanna ecosystems. Tropical species occurred up to 500 km north of their present-day distribution, especially in humid depressions (Watrin et al. 2009). No analogue of this historic setting exists today. Large herbivores must have found excellent conditions in the early-Holocene landscapes of northern Africa and could expand their populations.

The period of Ancient Egypt, and the development of its high culture, is linked to remarkable climatic changes. The re-formation of the desert correlates with the establishment of settlements in valleys and the development of high civilization. With increasing aridification around 4000 BC, species that require large amounts of biomass necessarily had to move to the valleys. Since 2300 BC, arid conditions have prevailed and the availability of water was more and more restricted to the valleys. This must have caused increased encounters and conflicts between humans and large herbivore species.

Conclusion

Documents from archaeology and art can be valuable sources of ecological and biogeographical information. In particular, hunting scenes in Ancient Egyptian art represent a surprisingly precise reflection of the historic mammal fauna in north-western Africa. These pieces of art also demonstrate the regional (and part of the global) loss of vertebrate biodiversity. The scene in Medinet Habu (Thebes) even reflects the ecology and behaviour of extinct aurochs (*Bos primigenius*). Further hunting scenes include more species that are now

extinct in the wild (e.g. *Oryx leucoryx* and *Oryx dammah*) or subspecies that are globally extinct (e.g. *Alcelaphus buselaphus buselaphus*). These examples should encourage biogeographers towards more extensive use of historical sources of information.

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thesis abstract

The macroecology of island floras

Patrick Weigelt

Biodiversity, Macroecology & Conservation Biogeography Group, University of Göttingen, Göttingen, Germany; pweigelt@uni-goettingen.de

Abstract. Islands are key model systems in biogeography and ecology. However, standardized data on environmental characteristics of the large number of islands worldwide have so far been lacking, and the effects of these characteristics on island ecology and biodiversity remain insufficiently understood. In my PhD thesis, I presented the first comprehensive environmental characterization of the world's islands, covering past and present bioclimatic and physical island characteristics (including the spatial setting of islands and archipelagos). I used these data to investigate how island characteristics influence the diversity and assembly of island floras at different spatial scales and across major plant groups. To this end, I assembled a global database of vascular plant species composition including 45,000 species and covering 1,070 islands. I showed that different aspects of island environments affect different facets of insular diversity (species richness, turnover, phylogenetic diversity) across scales and major plant groups, in accordance with their predominant dispersal- and speciation-related traits and adaptations to climate. The results contribute to a better understanding of the environmental and evolutionary drivers of plant assemblage composition, on islands as well as on mainlands.

Keywords. Beta Diversity, Dispersal, Environment, Island Biogeography, Isolation, Phylogenetic Structure, Speciation, Species–Area Relationship

Islands have intrigued biogeographers since the beginning of biogeographic research (e.g. Wallace 1880) and have inspired some of the most influential theories in ecology and evolution (e.g. MacArthur and Wilson 1967). Physical island characteristics, like their discrete boundaries and isolated nature, make islands excellent ecological model systems (Whittaker and Fernández-Palacios 2007). However, synthesis and comparative research in island biogeography have been hampered by the difficulties inherent in collecting standardized data on the world's thousands of (mostly very small) islands. Such data are crucial not only for advancing biodiversity research, but also for understanding and facing the increasing threats to island biodiversity like species invasions and climate change (Wetzel et al. 2013, van Kleunen et al. 2015). In my PhD thesis (Weigelt 2014), I therefore provided an environmental characterization of the world's islands and investigated how island characteristics relate to the diversity of island floras at the global scale. First, I focused on past and pre-

sent bioclimatic and physical island characteristics (with emphasis on the spatial setting of islands and archipelagos) as drivers of plant diversity; and second, I focused on taxon-specific, trait-related differences in the response of diversity patterns to abiotic factors.

In order to provide a rigorous and standardized bioclimatic and physical characterization of the world's islands (Weigelt et al. 2013), I calculated physical island characteristics using global coastline data¹ and digital elevation and bathymetry models (Hijmans et al. 2005, Amante and Ekins 2009) for 17,883 of the world's islands larger than 1 km². These characteristics were: area, distance to the nearest mainland, the land area as a proportion of total area of buffers (of 100, 1,000 and 10,000 km) surrounding the island perimeter (hereafter 'surrounding land area'), maximum elevation, and connection to mainland during the last glacial maximum (LGM). Furthermore, I calculated annual means and variability in temperature and precipitation using WorldClim data (Hijmans et al.

¹ GADM database of Global Administrative Areas, Version 1; www.gadm.org/version1/; last accessed 16 June 2010

2005) and climate change velocity in temperature since the LGM, i.e. the speed that a species has to move to keep up with climate change when considering topographic heterogeneity (Sandel et al. 2011). Using ordination and clustering techniques, I then characterized the world's islands in multidimensional environmental space. To showcase the usefulness of such a global data set, I made global predictions of insular vascular plant species richness. Species numbers for training the model were partly derived from a newly compiled and uniquely comprehensive database of 1,295 island plant checklists, including c. 45,000 native vascular plant species (Fig. 1). In contrast to existing datasets on island plant diversity, this is the first global one that includes actual species identities, enabling me to investigate species turnover among islands and phylogenetic diversity patterns at a global scale.

To address the roles of different aspects of island isolation in determining insular species richness I compared ecologically meaningful metrics of island isolation in models of vascular plant species richness (Weigelt and Kreft 2013). Despite the long-known, widely accepted importance of island isolation as a driver of immigration and speciation (MacArthur and Wilson 1967), the different facets of isolation – including stepping stones, surrounding landmass, wind and ocean currents, and climatic similarity between islands and mainlands – have only been addressed in a few case studies (e.g. Muñoz et al. 2004, Diver 2008). I therefore developed a set of 17 isolation metrics in 68 variations, calculated with accurate coastline data¹, and evaluated their explanatory power for vascular plant species richness for 451 islands worldwide. I hypothesized that the proportion of variation in species richness explained by isolation is higher when considering large source islands, stepping stones, climatic similarity, wind and ocean currents and the total area of surrounding landmasses, as opposed to considering only the commonly used metric of distance to the nearest mainland.

In addition to the degree of isolation of single islands, the spatial arrangement of islands within archipelagos should affect different aspects of diversity, such as the diversity of entire archipelagos (γ), the diversity of their constituent islands (α) or turno-

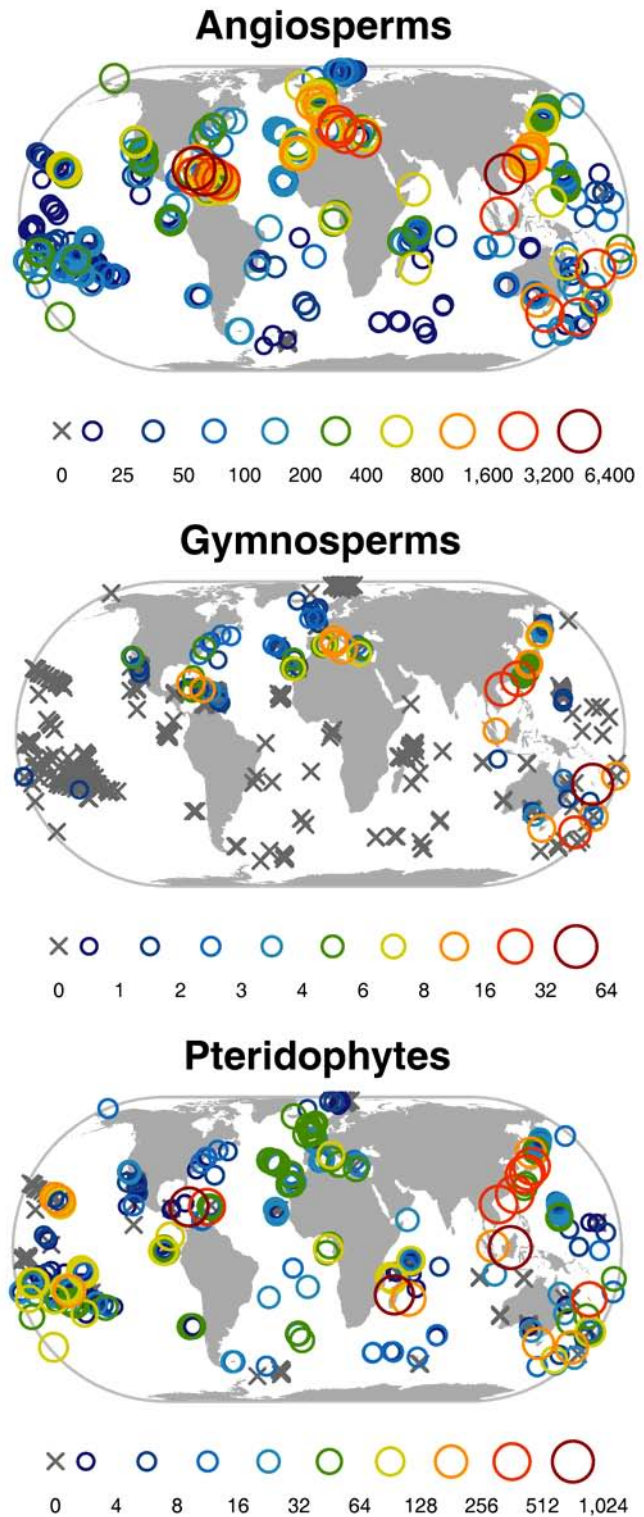


Figure 1. Species richness of native angiosperms ($n = 672$ islands), gymnosperms ($n = 666$) and pteridophytes ($n = 605$) on islands worldwide, derived from the global database of species checklists developed for my thesis. The database comprises 1,295 checklists for 1,070 islands or island groups and includes 45,000 native vascular plant species. Only islands with comprehensive checklists for the given taxon, including information on floristic status (native vs. introduced), are shown here.

ver among their islands (β) (Cabral et al. 2014). My colleagues and I investigated these three diversity components for the vascular plants on 23 archipelagos worldwide, and the extent to which they can be accounted for by biogeographic predictors (such as area, isolation and age), bioclimatic predictors and intra-archipelagic spatial predictors. We hypothesized that α is mainly driven by biogeographic and climatic determinants, that β is influenced mainly by the intra-archipelagic spatial structure, and that γ is mainly affected indirectly, i.e. through biogeographic, climatic and intra-archipelagic factors influencing α and β . We developed a set of predictors describing the intra-archipelagic spatial structure, including mean inter-island distance, connectivity, total archipelago area, range in island areas and the environmental volume occupied by an archipelago's islands as defined by the global bioclimatic and physical principal components analysis from Weigelt et al. (2013). We used multi-model inference to assess variables' importance in linear multi-predictor models, and structural equation models to test for the hypothesized indirect effects.

Island area, isolation and macroclimate are strong predictors of plant species richness at the island and archipelago level (MacArthur and Wilson 1967, Kreft et al. 2008), but it is unclear to what degree physical island characteristics predict species richness at a local, plot-level scale. My colleagues and I therefore tested whether area and isolation, the main physical island attributes considered by the equilibrium theory of island biogeography of MacArthur and Wilson (1967), can explain species richness at the plot level (Karger et al. 2014). We hypothesized that island area and isolation are important predictors of plant diversity only at large grain sizes and that their effects are diluted at small grain sizes (plot level) where local environmental conditions limit species diversity and communities may be saturated. We used field data on fern species richness in mountain forest plots on twelve islands in Indonesia and the Philippines (Karger 2013) to test for relationships between species richness and island area, isolation and macroclimate, as well as local environmental conditions, at grain sizes ranging from small plots to entire islands. For this analysis, we

used simple linear models and relative importance metrics.

Major groups of land plants differ in dispersal abilities and levels of gene flow, speciation rates and adaptations to climate (Donoghue 2008). Physical island characteristics may therefore affect different groups of organisms in different ways. To address this my colleagues and I tested whether major land plant groups differ in their species–area relationships (SAR) on islands and continental settings (Patiño et al. 2014). We expected that the geographic remoteness of oceanic islands would result in SARs with lower intercepts and a steeper slopes than SARs on continental islands, which would themselves have lower intercepts and steeper slopes than SARs of mainlands. We further hypothesized that SAR slopes and intercepts should increase from bryophytes to pteridophytes to spermatophytes because of decreasing dispersal abilities. We tested these hypotheses using a linear mixed-effects modelling approach, modelling variation in species richness as depending on area across geological systems and taxonomic groups.

To address how dispersal and environmental filtering in combination with *in-situ* speciation affect the composition of island assemblages, I again performed a cross-taxon comparison and studied phylogenetic structure of fern, angiosperm overall and palm assemblages (Weigelt et al. 2015). Traits related to dispersal, gene flow and adaptations to climate are often more similar among closely related species than expected by chance (Donoghue 2008). I therefore hypothesized that, when accounting for species richness, (a) phylogenetic diversity should decrease with environmental factors that increase chances of dispersal to islands; (b) phylogenetic diversity should be higher under environmental conditions that fit the bioclimatic requirements of more major lineages; and (c) phylogenetic diversity should decrease with factors increasing the probability of *in-situ* speciation on islands. I expected these relationships to be less pronounced for ferns than for angiosperms or palms (in particular) because ferns tend to have higher dispersal ability, wider distribution ranges and more frequent speciation through hybridization and polyploidization (Kessler 2010). Using generalized additive models, I investigated pat-

terns of phylogenetic diversity based on dated phylogenies for 393 islands and 36,297 species using deviations from null expectations in phylogenetic diversity and structure of island floras in relation to island area, isolation, geologic setting, island age, environmental heterogeneity, past and present climate, size of the source pool and biogeographic history.

Results and Discussion

Altogether, my research shows how island characteristics (e.g. past and present climate or the spatial island setting) relate to different facets of insular diversity (species richness, turnover, phylogenetic assemblage structure) across scales (archipelago, island and plot-level) and major plant groups (e.g. bryophytes, ferns, seed and flowering plants).

The island characterization provides the first quantitative evidence that, globally, islands differ from mainland areas in their bioclimatic and physical characteristics (Weigelt et al. 2013). Islands are, on average, significantly cooler, wetter and less seasonal than mainlands. Because of their typically small size, they are less topographically heterogeneous. Wet temperate climates, which support temperate rainforests (one of the rarest ecosystems on Earth; Olson and Dinerstein 2002), are more prevalent on islands.

The new collection of physical island characteristics that I compiled, especially the quantification of island isolation and position relative to other islands and the mainland, allowed me and my colleagues to do thorough analyses of putative determinants of island plant diversity patterns. At the global scale, isolation was ranked as the second most important factor (after area) determining vascular plant species richness on islands (Weigelt and Kreft 2013). Using ‘surrounding land area’ as the isolation metric gained highest model support, suggesting that surrounding landmass is important as a source of constant recolonization (‘rescue effect’; Brown and Kodric-Brown 1977). These results are in line with findings at smaller spatial extents (Diver 2008) and for habitat islands (Fahrig 2013). Also, the explanatory power of isolation for species richness increased when consid-

ering stepping stones, large islands as source landmasses and climatically similar source landmasses, compared with using the distance to the nearest mainland. I also showed that isolation was ranked as less important for large islands, where *in-situ* diversification is thought to counteract the negative effect of island isolation on immigration (compare Kisel and Barraclough 2010).

At archipelagic scales, aspects of intra-archipelagic spatial structure, particularly mean inter-island distance and range in island areas, were important in the models for β -diversity and, through β , for γ -diversity of vascular plants (Cabral et al. 2014). In the models, γ -diversity was mainly determined by indirect abiotic effects via α and β , with β being the more important component. These results suggest that mechanisms like *in-situ* diversification and island-hopping (Gillespie and Roderick 2002, Losos and Ricklefs 2009), which may drive patterns of β and γ -diversity on oceanic archipelagos, are linked to the intra-archipelagic spatial structure. These findings again highlight the importance for island biodiversity of physical island characteristics, in this case the location of islands relative to one another, and indicate the necessity of considering islands in an archipelagic context in island research.

However, the importance of physical island characteristics for diversity is thought to gradually decrease with spatial grain size (Karger et al. 2014). Consistent with island biogeography theory (MacArthur and Wilson 1967), my colleagues and I found strong correlations between fern species richness and both area and isolation only at the island level. In contrast, diversity at the plot level was mainly related to local environmental conditions. This is probably because local diversity is more saturated than diversity at large grain sizes, constraining the number of species from the species pool that can enter local communities (Fox and Srivastava 2006). To understand local diversity on islands, it is hence important to consider scale-dependent species pool effects (Karger et al. 2014).

The comparative cross-taxon analyses revealed clear differences among major plant groups in the correlations between putative envi-

ronmental drivers and both species richness and phylogenetic diversity (Patiño et al. 2014, Weigelt et al. 2015). As expected, my colleagues and I found an increase in SAR slopes from mainlands to continental islands to oceanic islands, and an increase in SAR slopes from bryophytes to pteridophytes to spermatophytes – though only for oceanic islands. Intercepts decreased from continents to continental islands to oceanic islands and from spermatophytes to bryophytes to pteridophytes (Patiño et al. 2014). These results challenge recent findings by Aranda et al. (2013), who found no differences in SARs among Macaronesian plant groups with varying dispersal ability and suggest that island assemblages of spore-producing plants are not always less species rich than continental assemblages (Patiño et al. 2015).

Furthermore, my models suggested that physical and bioclimatic island attributes, via their effects on environmental and dispersal filtering and speciation, determine the phylogenetic structure of island floras (Weigelt et al. 2015). Environmental predictors explained more variation in phylogenetic diversity and clustering for angiosperms and palms than for ferns, in accordance with expectations based on the high dispersal ability and large biogeographic ranges typical of ferns (Kessler 2010). When accounting for the effect of species richness on phylogenetic diversity, phylogenetic diversity was negatively related to isolation for palms but positively related for angiosperms, probably reflecting the immigration of angiosperm lineages from different biogeographic regions with distinct evolutionary histories to highly isolated islands. For both angiosperms and palms, phylogenetic diversity was negatively related to island area, suggesting an effect of *in-situ* speciation on large islands (Davies and Buckley 2011). However, in angiosperm assemblages mean-pairwise phylogenetic distances were also greater on large islands. This might be due to many angiosperm lineages with few or no speciation events and only a few large radiations on very large islands, which are mainly of continental origin (Weigelt et al. 2015).

Islands harbour large numbers of endemic species (Kier et al. 2009) and their biota

are threatened by habitat loss, biological invasions and changing climate (Kier et al. 2009, Wetzel et al. 2013, van Kleunen et al. 2015). The environmental characterization of the world's islands and the accompanying data and regionalizations presented in Weigelt et al. (2013) may serve as a spatial framework for macroecological research and conservation prioritization. My research demonstrates that accurate data on physical island characteristics are needed, for example to tackle such complex concepts as island isolation and intra-archipelagic spatial structure. Despite the long-appreciated importance of area and isolation for island species-richness patterns (MacArthur and Wilson 1967), ecologically meaningful descriptors of island isolation and intra-archipelagic structure have been lacking. The suite of metrics presented in my PhD research fills this gap and implies that a variety of colonization and inter-island migration mechanisms influence plant diversity patterns on islands and archipelagos at macro-scales (Weigelt and Kreft 2013, Cabral et al. 2014). The metrics should facilitate further research in island biogeography and could also be applied in related fields, such as research on habitat fragmentation (e.g. Fahrig 2013).

The database of island plant species' identities (Fig. 1) allows global analyses of patterns and putative drivers of biodiversity beyond species richness including β and phylogenetic diversity (Cabral et al. 2014, Weigelt et al. 2015). These facets of biodiversity have received increasing interest during the last few years (Beck et al. 2012) and are important for understanding the origin of global biodiversity patterns. Many relationships, such as the latitudinal beta diversity gradient and the relationship between functional and phylogenetic diversity, are still insufficiently understood (Fritz and Purvis 2010, Kraft et al. 2011, Tuomisto and Ruokolainen 2012). Islands may be key to answering some of the most compelling macroecological questions and the species database presented in my thesis, in combination with high-resolution phylogenies and information on species traits, will be supportive in this regard. As a start, I showed that relationships among environmental drivers and

species richness, as well as phylogenetic community attributes, vary among taxonomic groups in accordance with their predominant dispersal- and speciation-related characteristics (Patiño et al. 2014, Weigelt et al. 2015). This is a relatively new perspective in island biogeography and allows inferences about underlying processes affecting island diversity, such as dispersal, environmental filtering and speciation.

In conclusion, my research contributes to a better understanding of the composition of plant assemblages in relation to plant physiological constraints and the abiotic environment in general, on mainlands and on islands. Understanding how the diversity of contrasting plant groups has originated from immigration and diversification may further help to elucidate how global diversity patterns came about. Islands may play a key role in achieving this goal.

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Coastal conservation

Coastal Conservation. Brooke Maslo and Julie L Lockwood (editors), 2014, Cambridge University Press, 382 pp. £65 (Hardback) / £35 (Paperback) ISBN 9781107022799 / 9781107606746; <http://www.cambridge.org>

With the growing interest in marine, and especially coastal environments, Coastal Conservation – edited by Maslo and Lockwood – is a very timely volume. Comprising thirteen chapters, split into three parts, this volume examines the biodiversity status of coastal habitats and some of the emerging threats placing coastal biodiversity at risk.

Starting with some broad definitions, the opening chapter covers coastal conservation, biodiversity, ecosystems and ecosystem services, ending with what the authors call the *Coastal Conservation Gestalt* – an holistic overview of the breadth and complexity of the subject spanning species biodiversity, loss and degradation, and management which serves to encapsulate the overall thesis.

The following chapters illustrate the theme of the book with the aid of six examples of coastal environments: mangroves, beaches and dunes, seagrass meadows, oyster reefs in estuaries, dune forests, and salt marshes. The chapters cover threats to biodiversity and ecosystem services, status and trends, ecology and health, food security, drivers, spatial patterns, landscape ecology, complexity and fragmentation, pressures and biological responses, management, challenges, legislation and policy. They also suggest the way forward in terms of solutions such as restoration, conservation, the need for a global approach, and the need for future research.

The second part of the book then extends this further to consider emerging threats, which naturally include climate change, but also invasive species, the impacts of oil spills, and the over-exploitation of coastal environments. The main message throughout is a need for more research to enhance our current knowledge and understanding of the effects that each threat will have on biodiversity, the coastal environment, and its management. This will be necessary if we are to implement and improve coastal conservation practices.

The final section of the book provides a very valuable chapter which serves to pull together the themes touched upon in each of the preceding chapters. Whilst it is clear that we already know a lot about coastal biodiversity, it is also clear that there are many questions still needing answers. Species loss and habitat degradation are identified as being a very real feature of many coastal environments around the world. We are seemingly aware of the need to act on conservation but there are still substantial challenges and gaps in our knowledge. It is also argued that to date we have paid inadequate attention to coastal biodiversity, and there is now a very real need to expand our conservation activities around the world. One of the problems facing existing approaches to coastal management is that they are all too often related to legal and administrative boundaries that treat the land and oceans as independent units. Coastal biodiversity is still not yet an integral consideration in many approaches to management. Habitats are not simple, and the connectivity of the ecosystems is important in relation to coastal management as some species only spend part of their life cycle in one system then move to another. In addition, the paucity of coastal endemics has meant relatively little attention has been paid to coastal ecosystems.

Although we have developed the capacity to collect environmental data and information for monitoring and mapping at many different scales, there is still a scarcity of high resolution spatial data at the local scale, and a lack of baseline data, which are essential for monitoring. Treaties and instruments do not always provide for legal protection and there is still a lack of strong legislation. In addition research, education, knowledge, understanding in the widest context, and appreciation are important. There is also a need for a more global approach to monitoring, inventory, research, integration, international cooperation, and awareness raising. If we are to focus on

coastal biodiversity and coastal conservation then it needs to be placed in the context of sustainable long-term exploitation of the marine environment taking account of people's needs. Responsibility must be placed on society to maintain the ecological properties of these systems and to commit the will and resources to conserve them into the future. Our lack of understanding about the effects of climate change on marine life also needs to be tackled, and whilst managing for climate change is essential we need to have more certainty about the direction and magnitude of climate change to begin with.

In the Synthesis, amongst other things, the authors also touch further upon ecosystem function and services, with a reminder about the concerns for the loss and degradation of coastal ecosystems and the social and economic importance that these ecosystems provide. There is a need to consider the complexity of conserving and managing coastal ecosystem services in light of the expansion of urban settlements at the coast, particularly in relation to the scale of and need for coastal modification through protection against the impacts of climate change. As coastal development is often not designed to conserve or promote ecological processes there is a need to treat coastal infrastructures as habitat and to recognise connectivity between the coast, land and sea.

A statement by the editors at the end of this book, one that is very fitting and serves to emphasise the importance of marine and coastal environments, is "there is something special about coasts". Coasts are indeed special environments with a unique character and existence, and environments that are under growing pressure from human activities necessitating various different management approaches. Although attention to the conservation of coastal and marine environments has grown in the last decade, there is still a need to develop a far greater knowledge and understanding of the living component, one that is crucial to our continued and sustainable use of this special environment and particularly in light of climate change.

This book is very well-written and structured. It is also nicely produced, and illustrated,

although the overall appearance of the volume is a little conservative and rather dated. The book includes some black and white illustrations which are also duplicated in colour in the centre section of the book. I am not quite sure why the illustrations are produced in both black and white and colour, as one or the other would have been adequate. Whilst placing colour illustrations in the centre section of a book is still quite common it is a pity that they could not just have been integrated into the main body of text in colour in place of the black and white ones. Each chapter also includes a comprehensive list of references, contributors and abbreviations, all useful additions which are both helpful and add value. Although not really a textbook suitable for an undergraduate course, this volume would undoubtedly provide an excellent resource for a more advanced class or an MSc programme module.

A final observation: there is an awful lot of information and ideas to take in when reading this small book for the first time, and it is clearly much bigger on the inside than it appears on the outside. Coastal Conservation most definitely warrants a place on the bookshelf and opening more than once.

David R. Green

School of Geosciences, University of Aberdeen, UK

<http://davidrgreen.org.uk/>

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Edited by Markus Eichhorn

A path through the tangled bank

Ecology of Lianas. Stefan A. Schnitzer, Frans Bongers, Robyn J. Burnham and Francis E. Putz, 2014, Wiley-Blackwell, 504 pp. £95.00 (Hardback) / £85.99 (E-book) ISBN: 978-1-118-39249-2 / 978-1-118-39248-5

Lianas are a neglected form of plant life. Foresters despise them, hacking them out of plantations and concessions. Logged and secondary forests are choked with impenetrable thickets of lianas. To a rain forest ecologist they are an inconvenience, as determining the rooting points of looping, forking stems is a nightmare. Whole clumps fall from the canopy and block paths like suspended Gordian knots. Traces of vestigial chauvinism creep through occasionally in this book where authors use terms such as 'liana infestation' to describe explosive increases in abundance. Much evidence exists of the impacts of lianas on trees, yet I found no studies regarding the reciprocal effects of trees on lianas. Old prejudices die hard.

Lianas are woody climbers acting as structural parasites on trees and shrubs. By investing fewer resources in self-support, they are able to maintain high leaf areas for a given stem size, and thereby have an effect on forest productivity which outweighs their biomass – they can reach the canopy with stems only a tenth the size of trees. On Barro Colorado Island (Schnitzer et al., chapter 7) lianas are present on almost half of trees, make up a quarter of the stems above 1 cm diameter and a third of woody plant species richness, but only 3% of biomass. Compared to trees they have greater amounts of storage parenchyma, longer and wider water-conducting vessels and deeper roots. These provide an advantage in dry conditions, which contributes to their abundance in seasonally dry forests and the environments created by disturbance or fragmentation. The cost is an increased risk of cavitation in wide xylem vessels which likely constrains their distribution when minimum temperatures fall below freezing.

The lianaceous habit has many independent evolutionary origins across the angiosperms, along with a number of gymnosperms, and even extinct ferns. As Burnham (chapter 16) reveals, there were already lianas in mid-Devonian forests 398–385 Mya climbing the fern-like trees. They have therefore been a component of forests almost from the very beginning.

The study of itself lianas has a noble ancestry; Darwin himself wrote a treatise “on the movements

and habits of climbing plants” (Darwin 1865). Yet it is only since the 1980s that ecologists have begun to regard lianas as a fundamental component of forest systems rather than aberrant curiosities. A collation of papers can be found at <http://lianaecologyproject.com>. Difficulties surrounding their measurement have been largely removed as a result of the publication of a standard protocol (Gerwing et al. 2006, Schnitzer et al. 2008). This has opened up the potential for comparative studies, and the most comprehensive previous treatment, Putz and Mooney (1991), was overdue an update.

The book is an edited volume of 30 chapters by a total of 84 authors, each a self-contained study with its own literature review and reference list. Almost all of the chapters meet a standard equivalent to a journal article, which is commendable, and a combined index helps track down specific themes. I even found myself enjoying chapters on liana wood anatomy, a topic which I'll confess to never considering before. Some are outstanding contributions to the literature in their own right; van der Heijden et al.'s chapter on the impacts of lianas on carbon storage in forests (Chapter 13) is worth the cover price alone and prompts many hypotheses which remain untested. For example, through higher turnover of leaves with high nutrient content, might lianas homogenise soil fertility across forests? Of all the chapters, Santiago et al. (Chapter 20) might make the most long-standing contribution by fixing an honest eye on the quality of the evidence behind many supposed mechanisms driving patterns of liana abundance. A number of cherished assumptions are ripe for scrutiny.

Biogeographers will find plenty of regional comparisons, though many of these are hampered by glaring gaps in the literature. If this book serves one function above all others then it will be to shine a light on the regions where little work has been done – only two sites in the whole African continent have received detailed study. Most biogeographers will turn directly to DeWalt's chapter (Chapter 11) on global patterns in liana abundance and diversity, and ponder some of the broader mysteries. Why is it that Asian forests contain only half the liana density of those in South American

and Africa? Is there a fundamental reason why Africa contains 50% more liana species than the neotropics and 140% more than Asia? Is the paucity of lianas in dipterocarp-dominated forests a cause or a consequence? Why are most neotropical lianas wind-dispersed, while in the palaeotropics animal dispersal assumes greater importance?

Given that regular fruit production by lianas makes them a valuable source of nutrition for many birds, primates and other species, it is likely that the repercussions of biogeographical patterns span whole communities. Lambert and Halsey (chapter 26) provide a thorough assessment of the hypothesis that relative liana abundance and diversity lies behind the preponderance of gliding mammals in southeast Asia versus those with prehensile tails in South America (Emmons & Gentry 1983). This is well-worn territory but their review provided a refreshing perspective. I wasn't won over by the conclusion that risk of falling lies behind the pattern (personally I favour the avoidance of ground-based predators), and the inevitable reliance on circumstantial and discursive evidence makes this an intriguing mystery.

One consequence of the format of the book is repetition across chapters, particularly in justifications for the study of lianas. There are also a few contradictions. Many of the chapters state firmly that liana abundances in tropical forests are increasing, and hence are an urgent priority for study. Most cite the final chapter of this volume as evidence (Schnitzer, chapter 30). Yet once one reaches the end it transpires that the evidence (though compelling) is confined to the neotropics. cursory mention is made of the absence of similar patterns in the small number of African studies (including one in this volume) or elsewhere. The chapter argues that disturbance is promoting increased liana abundance, yet also notes that increases are mostly observed in intact, old-growth forests. Lengthening dry seasons seem a more plausible driver and in line with the growth advantage which lianas have over trees in such conditions. I finished the book less convinced that lianas were taking over the world than when I first opened it.

In this final chapter, Schnitzer argues that an urgent priority should be a global network of large-scale, long-term monitoring plots to track changes in liana abundance. While we should always be in favour of

more data collection, without compelling evidence of consistent global-scale changes this sounds like a plea for a problem more than an answer. Perhaps a more realistic goal would be to convince existing forest plot networks (e.g. CTFs) to include liana censuses in their standard protocols. At present a lack of robust or extensive data constrains the conclusions which can be drawn on many issues.

I write this review from a field station in Western Uganda, where reading this book has opened my eyes to the central importance of lianas in forest structure and dynamics. The highest compliment I can pay it, however, is that it only took so long to review because my students kept borrowing it. If the aim of the authors was to inspire more studies of lianas and raise their profile then they have already succeeded. At the very least it will give you pause before swinging your machete.

Markus Eichhorn

The University of Nottingham, UK
markus.eichhorn@nottingham.ac.uk

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Edited by Joaquín Hortal

Lots of good fish in the sea

Fishes: A Guide To Their Diversity. Philip A. Hastings, Harold Jack Walker Jr. and Grantly R. Galland, 2014, University of California Press. 336pp. £24.95 (Paperback) / \$34.99 (eBook) ISBN: 9780520283534 / 9780520959330; <http://www.ucpress.edu/>

There is a range of excellent guide books out there for the budding non-academic ichthyologist, young student and more wizened academic. The majority however have been developed as field guides, with excellent colour photographs of the species in their natural habitat (where available) or at least with an apt description of their ecology. Hastings et al's '*Fishes A Guide to their Diversity*' is different, and has been developed for those students (and lecturers) that are interested in developing their knowledge of the morphology and taxonomy of fishes. In this respect, this book is an excellent and exceptionally accessible part of the 'toolbox of taxonomists' (Pante et al 2015).

A new student in taxonomy (or any new graduate student of ichthyology and morphology), will find a wealth of vital information on how to accurately describe and compare the various morphological characteristics that synonymise different families of fishes. For beginners, however, I would argue that there is utility in using this guide in conjunction with a well-illustrated field guide to provide a full sense of the major colour patterns that help to identify fish groups.

More experienced graduate student and early academics can use it a stepping stone to further their knowledge of the higher level taxonomy of fishes. In this respect, this was the first time I have seen the full oral and pharyngeal morphology of different fishes provided, which makes this is an excellent resource for examining the morphology of fishes by way of dissection. The book also makes excellent use of x-rays, with a range of full fish skeletons provided.

While this guide may not provide a substantial amount of new information for the senior ichthyologist, Hastings et al have included a much higher diversity of fishes than is usually encompassed within a guide book. The sheer diversity of deep water fishes, as well as descriptions and pictures of several obscure groups that are found in very specific habitats, makes this guide a useful

jumping off point for further research into such taxa.

While not shying away from using taxonomic language, the authors have provided excellent descriptions of each term, as well as clear pictures to illustrate where necessary. In this respect I found the book exceedingly useful – I remember being a young scientist starting out examining the morphology and ecology of small tripterygiid fishes in New Zealand and spending weeks searching obscure papers to compile a valid list of morphological characteristics (including internal bony structures) that could be used to compare between highly similar species. The authors done the work for us in this guidebook, providing an extensive array of morphological characters that can be usefully and easily utilised to compare the morphology of different fish species.

This book remains strictly within the confines of describing the adult form of all fishes listed. There would have been value in also illustrating and describing the body form, morphology and distinguishing characteristics of the juvenile and larval phases of all the fishes listed. I understand why the authors have chosen to restrict themselves to the adult life stage; juveniles have been woefully under-described, and are logistically harder to capture and curate (the same problems also manifest in curating and describing the larval forms of fishes). However, a guide to the diversity of fishes is lacking if it does not provide some description of their non-adult forms. Indeed, it is the larval stage on which the vast majority of research on tropical and temperate fishes has been focused, especially when attempting to understand the connectivity and dispersal of populations.

There is an acknowledged dearth of new, well trained and enthusiastic morphologists who can provide the necessary balance to the overwhelmingly use of molecular methods being used to determine the evolutionary relationships of

fishes. This imbalance is touched on within the introduction: “Too often, these molecular-based phylogenetic hypotheses are not supported by morphology, as the number of molecular-based hypotheses has far outpaced the ability of morphologists to fully explore them”. In this I agree wholeheartedly. We are now in an age where morphologists, and the vital taxonomic work that they do, are being outgunned by a new generation of molecular phylogeneticists. This book goes some way to make the morphological methods and analysis of fish taxonomy more accessible to a wide audience, and perhaps will inspire more to pick up a scalpel and tweezers and start delving into the diverse and exciting world of ichthyological morphology.

David Feary

School of Life Sciences, University of Nottingham

david.feary@nottingham.ac.uk

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Pante, E., Schoelinck, C., Puillandre, N. (2015) From integrative taxonomy to species description: one step beyond. *Systematic Biology* 64(1): 152-160.

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Books noted with interest

Mammals of Mexico

Gerardo Ceballos (editor)

2014, John Hopkins University Press, 984 pp.

\$150.00 (Hardback)

ISBN 9781421408439

<https://jhupbooks.press.jhu.edu>

544 species of mammal occur in Mexico—the second highest total of any country—and almost a third are endemic. This comprehensive, authoritative account neglects none of them, from manatees to the tiny volcano rabbit. The synthetic chapters are impressive in themselves, covering national patterns of diversity and conservation status. Species accounts include notes on taxonomy, natural history, associations with habitat types, elevational range, and distribution maps (with historical range when known). A dense, 80-page bibliography supports the text. An outstanding source of information for biogeographical research, and the photographs make it a pleasure to browse. Highly recommended.

Biogeography and Biodiversity of Cacti

Wilhelm Barthlott, Kerstin Burstedde, Jan L. Geffert, Pierre L. Ibisch, Nadja Korotkova, Andrea Miebach, M. Daud Rafiqpoor, Anke Stein & Jens Mutke

2015, Schumannia 7, 205 pp.

€39 (Hardback)

ISBN 978-3-7308-1144-3

<http://www.kakteen.org/schumanniae.shtml>

Although cacti are (almost) restricted to the New World, their 1438 species span 100 degrees latitude from boreal Canada to Argentine grasslands. Characteristic desert plants they may be, but species occur in habitats including high mountains and rain forests. A modern biogeographical treatment is long overdue. Seven centres of diversity are identified, yet no sign of a latitudinal diversity gradient is evident; instead two peaks occur at the tropics. Ranges of almost all species are mapped, in addition to richness at higher taxonomic and functional levels. The text is in both English and German, with sources drawn from both literatures.

The Evolution of Life

Graham Bell

2015, Oxford University Press, 496 pp.

£39.99 (Paperback)

ISBN 9780198712572

<http://oup.com>

Many of us struggled through interminable undergraduate courses which required memorising the features of obscure invertebrate phyla. This textbook is an antidote, focussing directly on the process of adaptive evolution and its effects upon populations. Given the broad sweep it is admirably concise, focussed and approachable. Each chapter follows a clear narrative thread, reinforced throughout. Two take a different approach, tackling the diversity and ancestry of life by working outwards from humans. Plants and fungi are barely mentioned, alongside other omissions, but if you want your students to gain understanding rather than simply rote learning then this comes highly recommended.

Discovering the Deep: A Photographic Atlas of the Seafloor and Ocean Crust

Jeffrey A. Karson, Deborah S. Kelley, Daniel J. Fornari, Michael R. Perfit, Timothy M. Shank

2015, Cambridge University Press, 430 pp.

£60 (Hardback)

ISBN 9780521857185

<http://www.cambridge.org/>

Given that the majority of our planet is covered in water, scientific sampling of the seafloor to date has been paltry. The frontiers of discovery in the abyssal depths pose as many technical challenges as extra-terrestrial space. This lavishly-illustrated book provides an introduction to deep sea discoveries, with a particular focus on mid-oceanic ridges and hydrothermal vents, which captivate geologists and biologists alike with their bizarre formations and associated species. This book functions as both coffee-table entertainment and entry-level textbook. It would be useful in tutorials as a source of illustrations, and will hopefully inspire a new generation of explorers.

The Great American Biotic Interchange: A South American Perspective

Alberto Luis Cione, Germán Mariano Gasparini, Esteban Soibelzon, Leopoldo Héctor Soibelzon & Eduardo Pedro Tonni

Springer Briefs in Earth System Sciences: South America and the Southern Hemisphere 2015, Springer, 97 pp.

£44.99 (Paperback) / £34.99 (eBook)

ISBN 978-94-017-9791-7 / 978-94-017-9792-4
<http://www.springer.com/>

A monograph documenting the extinction of mammalian megafauna in South America following the Great American Biotic Interchange. The earliest evidence of arrivals from North America lies in the late Miocene (c. 7 Mya), but the real exchange only began around 2.6 Mya and movement of taxa was predominantly southwards. The authors focus on chronostratigraphy and describing the geological record, omitting much contextual information regarding the habitats and communities within which these species were found and the wider repercussions of their loss. Despite its relatively short length the text is often repetitive and perhaps merited publication in a different medium.

Basic Steps in Geostatistics: The Variogram and Kriging

Margaret A. Oliver & Richard Webster

Springer Briefs in Agriculture

2015, Springer, 100 pp.

£44.99 (Paperback) / £34.99 (eBook)

ISBN 978-3-319-15864-8 / 978-3-319-15865-5
<http://www.springer.com/>

Geostatistics is an alternative tradition to those measures of spatial autocorrelation more typically used in ecology and biogeography, and perhaps underused as a consequence of relative unfamiliarity. Spatial covariance in a parameter is described using a variogram, which can be used to make predictions via kriging. This is particularly valuable when projecting in space from restricted sampling data, for example with environmental variables. This text provides a condensed introduction to the fundamental principles, albeit better suited to readers from a mathematical background than complete novices. No software tools are introduced and its greatest value may be as a concise reference.

Markus Eichhorn

University of Nottingham, UK

The SAGE Handbook of Biogeography

Edited by Andrew C Millington, Mark Blumler and Udo Schickhoff

This text is a manual for scoping the past, present and future of biogeography that enable readers to consider, where relevant, how similar biogeographical issues are tackled by researchers in different 'schools'.

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IX Spanish Congress of Biogeography

The IX Spanish Congress of Biogeography (7 to 14 June 2016) will focus on the theme "Distribution areas: between bridges and barriers" and aims to convene around the biogeographical science, in all its forms and applications, experts from very diverse geographical origins. You are invited to rethink and reinterpret the theoretical and methodological models that revolve around the extent and types of distribution areas. The exhibition of the latest results of the biogeographical multidisciplinary research at national and international level, and the discussion and exchange of ideas, will serve to take the pulse of the epistemological heart of Biogeography.

The scientific programme is currently being developed and will feature two-and-a-half days for communications and defense of exhibition posters. Authors should indicate a preference for the format of their contribution, although the Scientific Committee of the Congress will take the final decision. Priority for oral presentation will be given to those contributions that deal with the theme of the Congress. Each main author can register up to two communications. Other activities of the Congress will be a lecture and a roundtable discussion.

During the Congress, one day and an afternoon will be reserved for field trips and, post-congress there will be another three one-day trips, all through different Natural Areas of Betic-Rif mountain belts, around the Strait of Gibraltar:

1. South of the Iberian Peninsula (one day trip and one half-day trip during the Congress):

i. Torcal de la Utrera, Dunas de Matas Verdes and Paraje Natural "Los Reales de Sierra Bermeja"

ii. Natural Park Los Alcornocales and Natural Park del Estrecho.

2. Tangier Peninsula, northern Morocco (three post-congress field trips; each will last one day):

i. Natural Park Jbel Bouhachem

ii. Beni Bousera

iii. Talassemtane National Park

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The venue of the Congress will be Albergue Inturjoven Algeciras-Tarifa, Spain

(<https://www.inturjoven.com/albergues/cadiz/albergue-inturjoven-algeciras-tarifa>)

Pre-registration will be made through an online form available on the website of the Congress: <http://ugr.congressus.es/ceb2016>. Visit this website to get information about fees, publication of the results, the program, composition of the Scientific Committee and other practicalities.

Deadline for pre-registration and abstract submission will be December 31, 2015

job announcements

Postdoctoral researcher in Macroecology and Biogeography

The Biodiversity, Macroecology and Conservation Biogeography group at the University of Gottingen (Germany; www.uni-goettingen.de/biodiversity) is currently seeking a postdoctoral researcher. The full-time position is initially available for three years, can be extended for another three years after positive evaluation and should be filled as

soon as possible. The salary is defined according to the German E13 TV-L scale. The position involves a limited amount of teaching (4 credit hours/semester) and is suitable to develop an independent research profile and to gain experience in teaching and supervision that qualifies for a professorship. See more here for further information: <http://www.uni-goettingen.de/en/305402.html?cid=11020>



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