Marine biodiversity hotspots: What drives the higher biodiversity observed in the Indo-Pacific as compared with the greater Caribbean region?

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The biodiversity observed in the IWP is many times greater as compared with the GC. Turnover events in coral species have contributed to a less stable environment in the GC, in comparison with the IWP. Furthermore, the center of origin, accumulation, overlap and biodiversity feedback hypotheses try to explain this asymmetry in biodiversity of the two hotspots. Modes of speciation also give insights on the formation of biodiversity hotspots. This thesis examines the supporting evidence for these hypotheses. It is concluded that there is a much stronger biodiversity feedback in the IWP due to more peripheral areas, a stable environment as well as more species of important reef building corals.

Introduction

The mechanisms at work in centers of biodiversity have been interesting to biologists for over 100 years. "Single centers of creation" as Darwin (1859) first described them. There are two biogeographic realms in which the tropical marine environment is divided; the large Indo-West Pacific (IWP) and the smaller Greater Caribbean (GC). The larger IWP is considered the primary center of biodiversity, since it influences a very large geographic area, whereas the GC is considered a secondary center since its influence stretches out only into the tropical Atlantic(Briggs 2005a) .

The huge biodiversity difference can be seen by comparing the number of species present in each of these centers; the IWP has approximately 3000 species of fish and 450 species of coral, whereas the GC has approximately 700 species of fish and just 50 species of coral (Briggs 2005b).

Ecological factors such as habitat differentiation, reef area and geographical location play a big part in answering the questions in this thesis.

- What drives the higher amount of biodiversity seen in the IWP in comparison with the GC?

Divided in to sub-questions per section:

1. What were the geographical and evolutionary mechanisms involving the formation of the IWP and GC regions?
2. Which hypotheses explains the different biodiversity seen in the IWP and GC?
3. What modes of speciation are at play in the IWP and GC?

The question why there is such a huge difference in these two areas will be examined in this literature thesis, by using findings from different articles found on Web of Science. Terms of search were *origins of biodiversity Indo-West Pacific/ Caribbean,* further zooming in on *origination hypotheses* for both of the regions. *Biogeography* and *turnover history of the Indo-West Pacific* and *Caribbean* and *speciation in tropical hotspots,*. Most of these data are based on fossil records, phylogenies, molecular mechanisms and dispersal routes of species.

Many marine groups have the advantage of better dated fossil records in comparison with terrestrial groups. In fact, some fossil groups such as ammonites and trilobites have helped to develop some of the theories involving speciation(Miglietta *et al* 2011). Anthropogenic impacts and the need for conservation of these and other unique marine environments have shown the importance of understanding the diversity patterns seen in the IWP and GC (Tittensor *et al* 2010).

Coral species turnover dynamics through time in the IWP and GC regions

   Both the IWP and GC have a long history of geographic events that shaped the regions to what they are today. These events are of fundamental importance for understanding the species diversity, origins, evolutionary history and, not least, for maintaining the areas as biodiversity hotspots. This section will deal with the Cenozoic Era; which includes the Paleogene (65,5-23,3 Ma), Neogene (23,3-2,6 Ma) and Quaternary (2,6 Ma-present) geological periods. The Neogene is divided in two epochs; the Miocene (23,3 – 5,3 Ma) and Pliocene (5,3 -2,6 Ma). Especially these epochs in the Neogene periods are of importance to understanding the evolution of the biodiversity hotspots, since a number of geological events have taken place in that time.

   The Tethys Sea existed between the two major continents of Laurasia and Gondwana during the Mesozoic Era (250 – 65 Ma). In the period of the Paleogene the closure of Tethys Sea divided the Tethyan fauna between the modern tropical Atlantic and the Indo-Pacific regions (Bromfield & Pandolfi 2012).

The Indo-West Pacific region

   In the early Paleogene period Scleractinia (modern stoney corals) began to appear and provided much of the framework for the developing coral reefs. This was followed by a rapid increase in generic diversity in the IWP during the Neogene and high diversity of corals emerged (Bromfield & Pandolfi 2012). A study performed by Bromfield and Pandolfi (2012) to examine the evolutionary history of coral generic richness during the Neogene period in the IWP region, found two major faunal turn-over events (Fig.1, Bromfield & Pandolfi 2012).

   The first faunal turn-over event was an increase in origination during the Miocene, fourteen new coral genera arose. The second faunal turn-over event also resulted in an increase in origination, but in a stepwise manner. During the late Miocene and Pliocene nine new coral genera arose, while five coral genera became extinct. The second event was followed by another extinction event during the Pliocene, where another twelve genera became extinct (Bromfield & Pandolfi 2012). Bromfield and Pandolfi (2012) linked these episodes of origination and extinction to one or more physical factors such as plate tectonics, changes in worldwide sea level, ocean currents and/or temperature and climate changes. The first turn-over event coincided with the Middle Miocene Climatic Optimum (~15 Ma); warm temperatures and minimal global ice(Bromfield & Pandolfi 2012) followed by a period of cooling and developing ice sheets, caused by the formation of the Antarctic circumpolar current, and also a lowered sea level. These changing conditions lowered gene flow among coral populations(Bromfield & Pandolfi 2012) and so allopatric speciation, to

provide the increase in coral generic richness seen in the Miocene. A second event also contributed to the first faunal turn-over seen in the Miocene, namely the Great Mid-Miocene collision event . The Australian and New Guinea part of Gondwana collided with the Asian part of Laurasia, giving way to differentiation and fragmentation of coral reef habitat (Bromfield & Pandolfi 2012) leading to more diversification in coral genera. Though this event already began around 25 Ma, a significant part of this event occurred in the Miocene at around 15 Ma(Bromfield & Pandolfi 2012).

The second turn over event in the IWP (Fig.1 Bromfield&Pandolfi 2012), which included a pulse of extinctions at the end of the Miocene and Pliocene (7 Ma- 5 Ma)(Bromfield & Pandolfi 2012), did not coincide exactly with some tectonic event. However, the Indonesian Throughflow (at present a part of the upper global heat conveyor belt) was being restricted. This restriction peaked at around 10 Ma – 4 Ma(Bromfield & Pandolfi 2012), and might explain the pulse of extinction in the IWP area due to lowering sea temperatures, though no empirical evidence has supported this. Also the Pliocene Climatic Optimum began around 4,5 Ma – 3 Ma, the global temperature was considerably warmer then present (3 C° higher), as well as the CO_2 concentration (roughly 30 % higher than pre-industrial levels) and sea level as far as 20 m higher. But conditions changed at the end of the Pliocene (5 Ma -2 Ma), providing a more dryer and cooler climate (Rebesco and Camberlenghi 2008) resulting in the formation of ice sheets in the Northern Hemisphere, which might explain the extinctions during this second turnover event in the IWP (Bromfield & Pandolfi 2012). However, Siddal et al (2003)found that the IWP reefs crests adapted to the changes in sea level as it dropped and as it rose.

The greater Caribbean region

There are three major turnover events in the history of the GC region, both origination and extinction events (Fig.1, Bromfield&Pandolfi, 2012) The total number of genera increased from the early Eocene (middle Paleogene) to the Oligo-Miocene (late Paleogene to early Neogene) (50 Ma- 22 Ma). There was a minor drop in diversity but the number of genera remained constant throughout. During the Plio-Pleistocene (late Neogene to early Quaternary, 1 Ma-2 Ma) number fell to the point of current genera levels observed in the GC region today (Budd 2000). However, species diversity had several peaks and Budd (2000) states that these peaks were the result of origination events. The first during the Middle to Late Eocene (40 Ma-36 Ma). The second during the Late Oligocene to Early Miocene (28 Ma-24 Ma), and the third during the Late Miocene to Early Pliocene (7 Ma- 4 Ma)(Budd 2000). Species diversity increased from the Middle to Late Eocene to the late Oligocene (40 Ma-22 Ma), after this time period the dispersal from the Meditteranean ceased(Budd 2000) at 12 – 18 Ma due to the uplift on the Red Sea land bridge; which separated the Atlantic fauna from the Indian fauna(Floeter *et al* 2008). After the Early Miocene (22 Ma) species that first occurred in the Caribbean region had limited distributions, and were only confined in the Caribbean (Budd 2000). Also around 11 Ma the Amazon outflow of freshwater spanned ~2300km of the coast of South America, separating the Brazilian fauna from the Caribbean ones (Floeter *et al* 2008). Many species and genera originations that occurred were in the time interval of 7 Ma – 4 Ma, just before the closure of the Isthmus of Panama(Budd 2000).

There were also three main extinction events occurring in the Caribbean region at Early to Late Eocene, Late Oligocene and Plio-Pleistocene. These events coincided with environmental factors(Budd 2000). The Paleocene-Eocene Thermal Maximum (PETM) caused an increase in global temperature of about 5 C°, this due to massive releases of carbon. The large decrease in deep-sea carbonates caused ocean acidification and dissolution and lead to a global decrease or even disappearance of coral reefs (Jackson 2010). The Middle to Late Eocene extinctions coincide with a drop in global temperatures, and are seen as the reason for the extinctions in both marine and terrestrial biotas (Prothero 1994, Budd 2000). In the Early Miocene, increased upwelling and the following increased turbidity as well as decreased temperatures caused the second extinction event (Budd 2000). During this event, two species of *Acroporidae* (an important reef-building coral of the order Scleractinia) became extinct (Glynn & Ault 2000). The closure of the Isthmus of Panama (3,5 Ma) caused the isolation of the Atlantic from the Pacific (Jackson 2010). Upwelling, as well as primary productivity collapsed. During the Plio-Pleistocene the onset of Northern Hemisphere glaciations caused a drop in sea surface temperatures and because the dispersal pool was at an all-time low due to the changes caused by the closure of the Isthmus of Panama(Budd 2000), the third extinction event was set in motion. Again, one species of *Acroporidae* became extinct (Wallace 2012)

Around 2 Ma, the cold water Benguela Current also limited the dispersal from the southern Indian Ocean to the West Atlantic. Limited dispersal due to the two hard barriers (Isthmus and the Red Sea land bridge) and the two soft barriers (Amazonian filter and Benguela Current), and the fact that generic diversity is strongly correlated with the areal extent of the dispersal pool and distance between (meta)populations, species or genera may have a difficult time to recover from environmental changes(Budd 2000). Budd (2000) also states that the generic diversity is associated with biotic factors related to biogeography, such as dispersal, and that this is the most important factor influencing species richness and generic diversity.

The effect of the extinction events in the GC region can still be seen today, as many species now living in the Caribbean are a reflection of the effect of these extinctions, for example long lived taxa such as some species from the *Acropora* genus and of the *Montastraea* genus (Johnson *et al* 1995). During the Plio-Pleistocene species with long lived colonies and colony fragmentation were able to maintain the ecological structure of the reefs. Long lived species have a lower speciation and extinction rate, making them more resilient to a changing environment (Johnson *et al* 1995, Budd & Johnson 1999). After the Plio-Pleistocene changes the Caribbean fauna has remained unchanged, there were no new originations or extinctions nor any migrations after this faunal turnover event(Budd & Johnson 1999). Jokiel &Martinelli (1992) pointed out that there is no counter current flowing eastwards from the Caribbean to other tropical reef areas thereby possibly preventing much of the dispersal outwards from the Caribbean to peripheral areas(Jokiel & Martinelli 1992). Also, the speciation of corals seen in the Caribbean has not occurred to the extent seen in the IWP. There are 20 genera and 50 corals in the Caribbean versus the 450 species know in the IWP(Glynn & Ault 2000,Briggs 2005b).
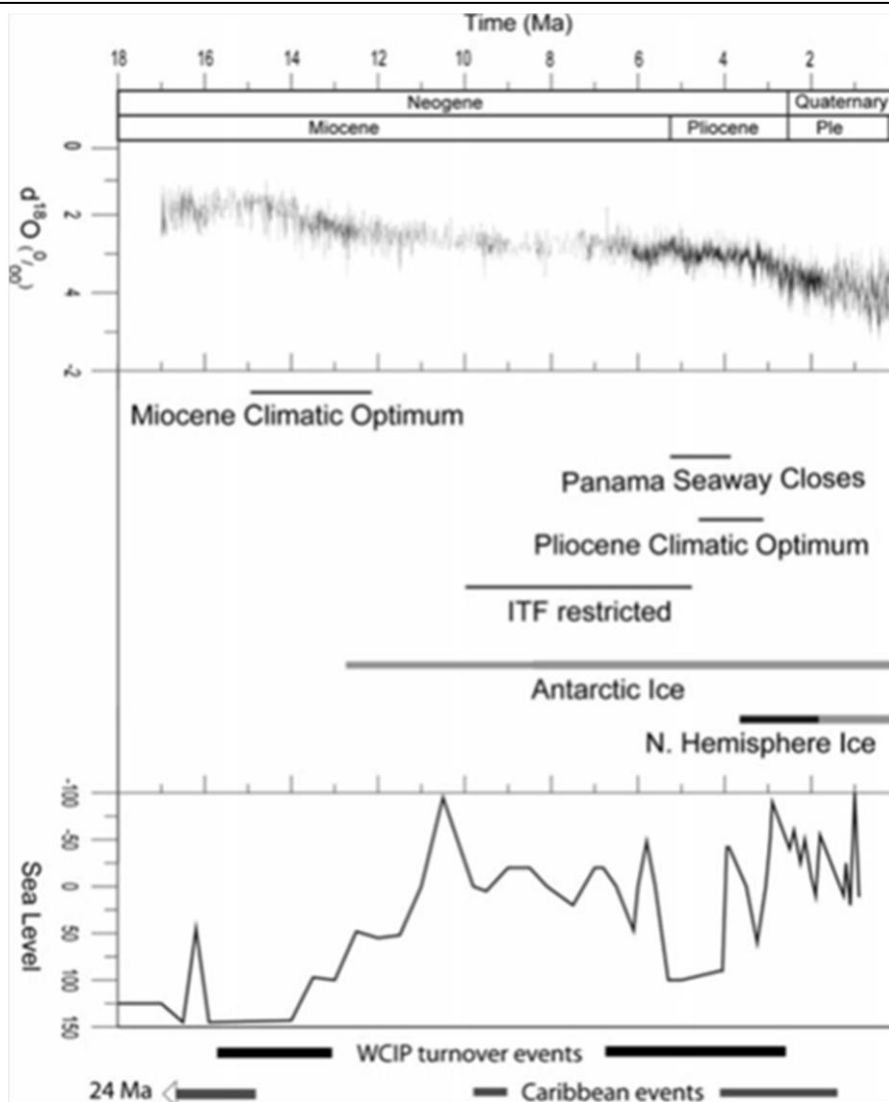
Fig. 1 Faunal turn over - and environmental events in the central IWP and Caribbean during the Neogene and Quarternary coral reefs. Oxygen isotope curve as a proxy for sea surface temperatures (Zachos et al 2001), sea level curves (Haq et al 1987).
Light grey bars represent permanent ice sheets, black bars represent temporary ice sheets at the poles (Bromfield & Pandolfi 2012).

Hypotheses about the origins of marine biodiversity hotspots

There has been much debate about how the biodiversity hotspots in the IWP and GC arose and how they function to this day. The first unified concept from centers of origin or centers of dispersal came from Darwin (1859). Species that dispersed away from this center had to overcome certain barriers and the age of taxa increased further away from the center (Mironov 2006, Briggs 1999,2005b). Opponents of this dispersal center hypothesized vicariance as a mechanism (Croizat *et al* 1974) in which the formation and disappearance of physical barriers are mainly responsible for the observed patterns as opposed to the species themselves dispersing (Mironov 2006). Modern genetic surveys clearly find a role of dispersal; and paleoreconstructions clearly support a role of barriers.

The historical "center of.." hypotheses tried to explain the huge biodiversity seen in the IWP and GC. However, as most scientists acknowledged, these hypotheses were not mutually exclusive. A new model, namely the biodiversity feedback, provided a synthesis between the three hypotheses (Bowen *et al* 2012, Rocha et al 2008).

<u>The Center of Origin/ Speciation hypothesis (CO)</u>
This hypothesis states that all new species arise in the biodiversity hotspot, expand their distribution range and slowly move outwards to the peripheral areas, replacing their ancestors . This means that the peripheral areas work as evolutionary sinks (Briggs 1974, Reaka *et al* 2008).

<u>The Center of Accumulation hypothesis (CA)</u>
The high number of species results from speciation in peripheral areas, ocean currents move them into the central area where these species accumulate (Ladd 1960, Reaka *et al* 2008, Halas & Winterbottom 2009).

<u>The Center of Overlap hypothesis(COverlap)</u>
The high biodiversity seen in the IWP is due to the overlap of the Indian Ocean fauna and the Pacific fauna. During low sea level, the Indo-Pacific barrier separated these faunas which , when isolated from on another diverged separately (Woodland, 1983)

<u>The Biodiversity feedback model</u>
This model incorporates the center of Speciation, Accumulation and/or Overlap hypotheses (Rocha *et al* 2008, Bowen *et al* 2012).

The Indo-West Pacific region
Recent studies of paleontological data and species histories concluded that the IWP was a CA from the Eocene on, but at the same time diversification and export of species took place (Cowman&Bellwood 2013).

Halas&Winterbottom(2009) tested multiple proposals for the origins of the Indo-West Pacific biodiversity by using a phylogenetic analysis for comparing trees (PACT). Although, using simplified models of the CO/CA and COverlap, their data falsified the CA and COverlap hypotheses and only found minor support for the CO hypothesis in two sister species pairs of combtooth blennies (*Plagiotremus spilistius* and *Plagiotremus iosodon*) and dottybacks (*Congrogadus subducens* and *Congrogadus hierichtys*)(Halas & Winterbottom 2009). These sister species pairs appear at a terminal node of the tree and are both found in the center of the IWP(Halas & Winterbottom 2009)..

Barber&Bellwood(2005) examined the evolutionary history of a reef fish, the wrass (genus *Halichoeres*), this genus (with 69 species) is highly abundant in the IWP as well as the GC. Barber&Bellwood(2005) tested for the CO, CA and C Overlap hypotheses but found limited support for the CO and the CA, but no support for the C Overlap concerning the IWP. The age of one of the two species of wrasses found at the peripheral areas was the oldest in the IWP clade(Barber & Bellwood 2005) , though this is in line with the CO, the other species at the peripheral area were relatively young, which in turn is concordant with the CA.(Barber & Bellwood 2005) However, these results can be explained by the biodiversity feedback model, since the results show characteristics of both the CO and CA.

The Greater Caribbean region

Rocha *et al* (2008) focused on the Atlantic reef fish the brown chromis (*Chromis multilineata*). Using patterns of genetic diversity (based on mtDNA sequences) dispersal routes could be found (Fig.2 Rocha *et al* 2008). His data showed that the Caribbean populations of brown chromis were the oldest, supporting the CO hypothesis. However, some of the Caribbean populations were derived from Brazilian lineages (based on haplotypes), supporting the CA hypothesis. In the past the GC has also acted as a CA, according to Barber&Bellwood (2005). One genus of gobies (*Gnatholepis)*, the anglerfish genus (*Centropyge)* and wrasses (*Halichoeres*) found in the GC, are derived from an IWP ancestor. Their phylogenetic data suggests that they dispersed from the East Pacific to the GC, before the final closure of the Isthmus of Panama (±3.1 mya).

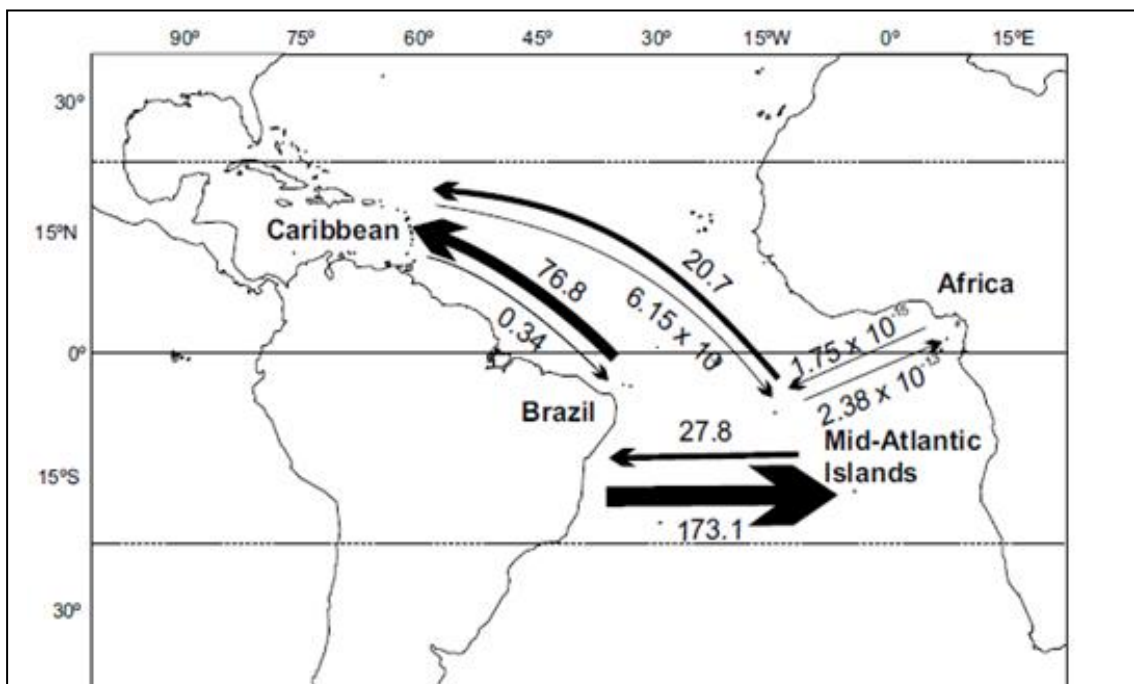When examining Fig.2 it is obvious that migration rates are higher towards the GC than

Fig. 2 Migration rates between populations of *C. multilineata* between the four tropical Atlantic biogeographical provinces. The thinkness of the arrows indicate the portion of migration proportional with the number above each arrow indicating migration (Rocha et al (2008)).

migration from the GC. Rocha *et al* (2008) argued that the higher migration rates towards the GC is a result of pelagic larval stages of most reef fish (and other species), and their dispersal depends on the duration of the pelagic larval stage and ocean currents. Most juveniles and adult reef fish remain stationary. The migration towards the GC is consistent with the general flow of the North Brazil current. Whereas, there is no countercurrent flowing away from the GC. Rocha *et al* (2008) concluded that there is a biodiversity feedback acting in the GC hotspot, the GC acted as a CO and CA, depending on the timeframe.

Another discussion about the origins of the GC biodiversity hotspot, is about relict vs colonization.

The relict hypothesis is based on the separation of the West Atlantic from the Pacific and eastern Indian oceans by the uplift of the Red Sea land bridge (12-18 Ma) (Floeter *et a*l 2008, Steininger&Rögl 1984). The colonization hypothesis is based on colonization events from the Pacific across the Eastern Pacific Barrier to the West Atlantic before the final closure of the Isthmus of Panama (±3.1 Ma), and/or colonization via South Africa (Floeter *et al* 2008).

These hypotheses give clear boundaries to test each hypothesis; if the relict hypothesis is true; species' age must be older than 12 Ma. If the colonization hypothesis (before the final closure of the Isthmus of Panama) is true, species must be younger than 12 Ma and older than 3.1 Ma (Floeter et al 2008, Coates&Obando 1996). Recent colonization (after the closure of the Isthmus of Panama)by species dispersal via South Africa; means that species must be younger than 3.1 Ma(Floeter et al 2008). In line with the relict hypothesis; an 18 Ma split in the wrasses phylogeny (*Halichoeres*) as well as an 20 Ma split in the genera of angelfish; *Holacanthus* and *Pomacanthus* was found, dividing the IWP clade and the Caribbean clade(Floeter *et al* 2008). Supporting the colonization hypothesis (via the opened Isthmus) a diversification in the wrass genera *Halichoeres* (Barber & Bellwood 2005, Floeter et al 2008), *Bodianus* (Bellwood 1994,Floeter *et al* 2008, Gomon 1997) and *Thalassoma* (Costagliola 2004) and for parrotfish genus *Scarus* (Bellwood 1994, Floeter *et al* 2008, Gomon 1997). However, Barber&Bellwood (2005) are cautious about supporting the colonization hypothesis, since their data suggests that a single colonization event happened in *Halichoeres*. Also, when including missing taxa into their data, the results show that the origins might have been entirely West Atlantic in this genus.

Mechanisms of speciation in the context of biodiversity hotspot formation

Many modes of speciation coincide with one or more hypothesis about the function and origin of the biodiversity centers. This paragraph will further investigate what kind of speciation occurs in the GC and the IWP hotspots.

Speciation modes which are considered present in a diversity center are; allopatric, parapatric. sympatric speciation (Briggs 1999) (Fig. 3) and surface circulation vicariance in corals (Veron, 1995). Furthermore, there are several models provided for modes of speciation; namely centrifugal speciation (Brown, 1957), peripatric speciation(Myr, 1954), ecological speciation (Via 2002) and ecological opportunity hypothesis (Simpson, 1953). Although some of these models are superseded, it points out the history of the debate about the dominant mode of speciation involving biodiversity centers.

Many of the hypotheses discussed in de previous paragraph; center of origin, center of accumulation, center of overlap and the biodiversity feedback hypothesis, have one or more distinctive modes of speciation, .

- The Center of Origin: This hypothesis depends entirely on sympatric speciation(Halas & Winterbottom 2009). Species are formed in the center, with relatively low dispersal rates. As the older species in the center expand their ranges, replacing the ancestral species in the peripheral areas. Sympatric speciation occurs when species' ranges overlap or are identical. Due to high competition, selection can occur which leads to reproductive barriers and eventually to diversification and the rise of a new (sister)species.

- The Center of Accumulation: Assumes that speciation can occur anywhere in peripheral areas, does not confine to one particular mode of speciation. Also, speciation rates are similar throughout the area. Post-speciation dispersal is mentioned by Halas&Winterbottom (2009); the species disperse/ are carried by currents to the center, after speciation has taken place.
- The Center of Overlap: Essential to this hypothesis is post-speciation dispersal with species originated through allopatric speciation at the seperated areas. Also recognizable by species pairs where one is only found in area #1 and the other only found in area #2(Halas & Winterbottom 2009).
- Biodiversity feedback: Incorporates all three "center of" models, hence allopatry and sympatry can both occur in this model (Rocha et al 2008, Bowen *et al* 2012).

Parapatric speciation and surface circulation vicariance are not explained in any of the hypotheses, but do occur in marine biodiversity hotspots. Parapatric speciation is defined by two or more subpopulation, living adjacent to one another, only connected by a small overlapping zone. In time, the two subpopulations may diverge due to reduced gene flow between the subpopulations, resulting in reproductive barriers.

Corals have weak reproductive barriers, allowing for interspecific speciation. These hybridization events play an important role in coral evolution (Veron, 1995, Willis *et al* 2006). The simultaneous mass spawning events in corals produces fusion and fission processes, depending on sea level and surface currents. This surface circulation vicariance model suggests that the timing and scale of these processes determines if a monophyletic group (which can be reproductively isolated) or a paraphyletic group is formed in corals (Veron, 1995).

Fig.3 four modes of speciation explained ((http://en.wikipedia.org/wiki/Speciation)
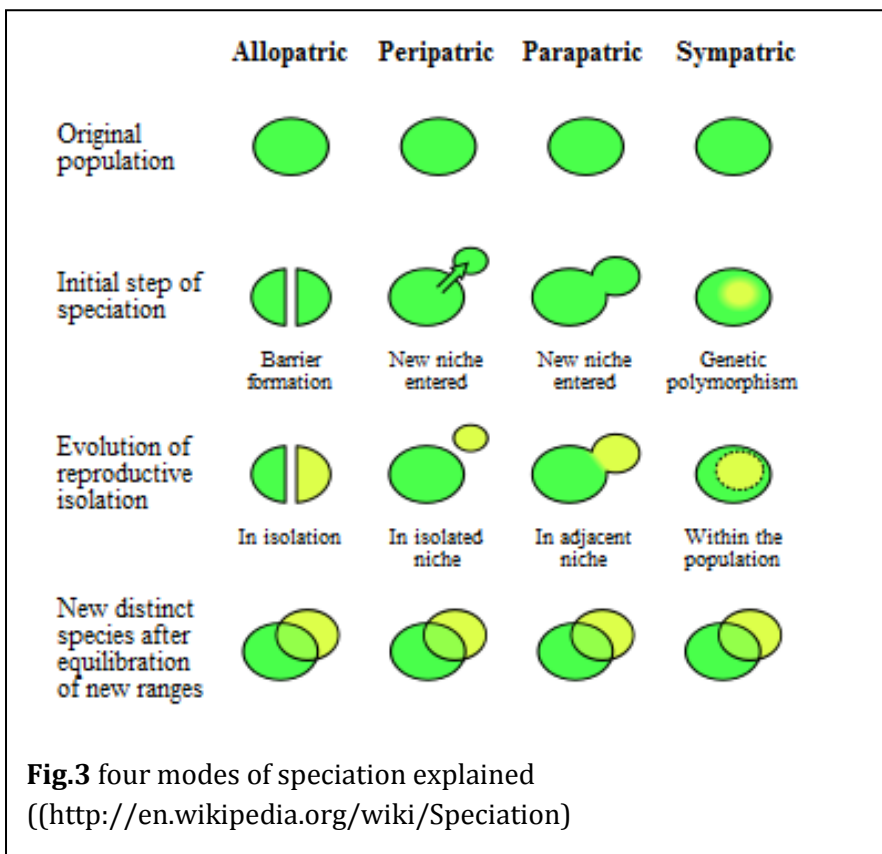
As stated by Briggs (2005,4); a center of origin depends on successful speciation in a competitive environment. A part from the mode of speciation, successful speciation also depends on the population size, genetic diversity and geographic ranges (Briggs 2005a) . Large populations tend to have a higher genetic variation (Briggs 2005a, Kimura &Ohta 1971), making them more resilient to changes, and better adaptable. Whereas smaller population may fail because of genetic drift; due to the random event of genetic drift, some important alleles may be lost, hence leave the population less well adapted to environmental changes.

Many scientists concluded that allopatric speciation may be the most dominant form of speciation concerning biodiversity center (Mayr 1963, Futuyma 1986, Paterson 1981, Briggs 1999)since it involves either dispersal or vicariance (Briggs 2005b).

Both vicariance and dispersal rely on lowered (or virtually zero) gene flow. A vicariant event happens when a population is separated by a newly formed barrier(Briggs 1999, 2005a, 2005b). Dispersal means that a population overcomes a barrier, also separating that population from the other, hence allopatric speciation occurs. (Briggs 1999). Described by Mayr (1954), the peripatric speciation model (see Fig. 3) depends on allopatric speciation, where small populations in peripheral areas supply the biodiversity seen in a hotspot (Mayr 1954,Briggs 2005a).

Although, previously thought to be the dominant mode of speciation; Briggs (2005a) believed that allopatric speciation in a wide geographic area, results in a mosaic of related species and subspecies; all byproducts of coincidental genetic divergence. These species don't tend to be very successful in further dispersing and producing successful phyletic lineages(Briggs 2005a) , and these species are all traceable back to one very widespread ancestor originated from the center of origin under competitive circumstances, hence sympatric speciation.

Sympatric speciation can occur very rapidly, much faster than allopatric speciation. Studies performed on this topic showed that (in the case of cryptic sea urchins) sympatric speciation can occur as fast as 250,000 years (Landry 2003). This speed of sympatric speciation has been contributed to the mechanisms behind this mode of speciation; the first step involves reproductive isolation by *selection* followed by speciation which is apparently completed very rapid (Briggs 2005b). Whereas allopatric speciation also works on reproductive barriers but *not by selection* but physical barriers separating populations, followed by slow speciation(Briggs 2005b). Since many species occur together in biodiversity hotspots, competition is very high which promotes sympatric speciation occurring alongside with allopatric and parapatric speciation (Briggs 2005a, 2005b). The concept of sympatric speciation is that sibling species occur in the same geographic, and are habitat-specific (Knowlton 1993)

Supporting the sympatric speciation mode, Brown (1957) constructed the centrifugal speciation model, this model is based on sympatric speciation and is applicable to centers of origins, explained in the previous paragraph. His model states that the more relatively advanced species (apomorphic) appeared in the center, while the more primitive species (plesiomorphic) were driven into peripheral areas(Briggs 2005a, 2005b, Brown 1957).

Ecological speciation (Via 2002) occurs when natural selection in different habitats, adjacent to on another, overrides gene flow. This is followed by reproductive isolation and eventually speciation (Rocha 2005)

Ecological opportunity hypothesis, first proposed by Simpson (1953) has recently been supported by empirical studies (Bowen *et al* 2012). Species in the biodiversity hotspot arise under intense competition which produces most of the diversification. However, species introduced to a peripheral area undergo an ecological release. There is less competition and allows niche expansion (Bowen *et al* 2012). Hence these two processes combined yield more biodiversity, than either process could alone.

The Indo-West Pacific region

Briggs (Briggs 1999, 2005a, 2005b) believes that all three modes of speciation occur in the IWP. Allopatric speciation occurs when species disperse or a vicariant event happens. The history of the IWP has shown that tectonic movement created many islands, where species disperse to and undergo allopatric speciation (Briggs 1999). Also, during the Pleistocene glacial, sea levels dropped, the shallow sea water habitats created vicariance events where again allopatric speciation occurred(Briggs 1999).

Parapatric speciation occurs mostly on the coastlines and were traditionally associated with planktonic species, however, evidence by Knowlton(1993) has shown that species of benthic organisms also show parapatric speciation due to different depth preferences (and so created adjacent populations)(Knowlton 1993). Briggs (1999) found that two pairs of sibling species of the butterfly fish (*Chaetodontidae*) have sympatric distribution, meaning that the ranges overlap partially or entirely. Vallejo(2005) found evidence for sympatric speciation in a clade of sea snails (Conus ebraeus). These sea snails occupy roughly the same geographic area but occur in distinct habitats, as is common in sympatric species (Vallejo 2005). However, Vallejo(2005) did not use a comparative phylogenetically based approach and so conclusions about finding sympatric speciation are premature (Halas&Winterbottom 2009). Halas&Winterbottom(2009) found 19 possible events of sympatric speciation in the genera of *Plesiops, Congrogadus* and *Plagiotremus* as well as the coral genera (*Acropora, Coscinaraea, Symphillia*). However, the coral species are so widespread that there is no reason to believe that they've all speciated within the IWP hotspot (Halas&Winterbottom 2009).

Greater Caribbean region

A study on wrasses (*Halichoeres*) perfomed by Rocha *et al* (2005) has shown that ecological speciation occurred among this species. Species of this genera show habitat preference and have specialized diets (*H.radiatus/brasiliensis* and *H.maculipinna*). This has also been seen in Atlantic surgeon fishes (Rocha et al 2002). As well as in gobies (Dawnson, 2002) and sea horses (Jones, 2003, Rocha et al 2005). Floeter et al (2008) emphasizes the effect of physical hard and soft barriers in the Caribbean region on the mode of speciation and believes that allopatry and parapatry together with ecological speciation due to habitat differentiation have led to diversifications(Rocha et al 2005).

Discussion

Miglietta *et al* (2011) are sceptical about sympatric speciation being more common than previously thought. Most work on sympatric speciation has been done comparing sister taxa range overlap, however, in the Pleistocene sea level changes occurred several times. Which means that most geographic distributions seen today are very recent and so false conclusions can be drawn concerning sympatric speciation when looking at range overlap. Simulations have shown that high rates of change in species range, makes it impossible to distinguish between modes of speciation. The shifting of species range may blur the geographic pattern of speciation, this also accounts for recent speciation events. Recent species diversifications can overlap their ranges and may show similar range overlap patterns with diversification of much older speciation events. This underlines the limitation

of phylogenies, used to examine speciation processes without taking into account the timing of the speciation events. (Quenouille et al 2011).

Many biogeographers use fossil records to trace back the age of certain taxa, however, fossil records are not always to be trusted. Since more than half of the classes of living organisms do not have any fossil record (Heads 2005). And so underestimations are made regarding fossil biodiversity.

Phylogeographers use both genealogies and molecular clocks. Molecular clock calibrations are a difficult measure as well, since most calibrations refer to other calibrations of mostly distant related taxa(Heads 2005). Clocks are usually calibrated by correlations of paleogeography (some unrealistic) or literal research of the fossil record(Heads 2005).
For example, the final closing of the Ishtmus of Panama (3.1 Ma) is used to describe the isolation and differentiation of the Pacific and Atlantic fauna, however this was not a singular event, but took millions of years. And Savin&Douglas (1985)referred to many opening and closings of the Ishtmus of Panama, thereby shifting the time of differentiation of the Pacific and Atlantic faunas(Heads 2005).

Mostly corals and reef fish have been used for biodiversity measurements since they are easy to census and relatively well known taxonomically. Though these taxa only represent a fraction of the biodiversity found in hotspots and therefore may not correctly reflect the biodiversity patterns across all organisms [57]. Measuring the biodiversity may require taking tissue samples of every taxon in clades inhabiting both of these areas. Once thought individual taxa might be cryptic species (Halas & Winterbottom 2009), which can lead to an underestimation of taxa or false conclusion in a taxon biogeography and dispersal.

Examining species or taxa individually might not explain the biodiversity in hotspots, rather looking at interactions between species, or symbiotic relationships, might reveal new insights on origination and maintaining biodiversity.

Conclusion

The fact that the IWP has a much higher biodiversity than the GC region is caused by the history of geological events. The IWP is much older, larger in area and more stable than the GC. Also the important key species of Scleractinia corals is more abundant in the IWP providing a more suitable environment for sustaining more biodiversity than the GC. This due to the turnover events in the late Oligocene/Early Miocene and the Plio-Pleistocene, which caused some of the species of Scleractinia to become extinct. The IWP has acted as a survival center for ancestral lineages, while elsewhere these lineages became extinct. This is the driving force behind the diversity seen today in the IWP (Cowman & Bellwood 2013). Furthermore the IWP has more peripheral areas and archipelagos than the GC providing more refugia and different habitats that promote biodiversity, acting as a center of origin as well as a center of accumulation, thus promoting the biodiversity feedback.
Dispersal from and to the IWP is much higher, there are less barriers that species must overcome then the species in the region of the GC.
New modelling techniques might reveal the timing of ceased gene flow and selection which lead to these evolutionary divergences (Bowen *et al* 2012).

The reason why biodiversity hotspot are of such interest to scientists is that they provide most of the species in the oceans worldwide and thus provide an incentive for protection. Fisheries, pollution, habitat destruction and climate change endanger these areas disproportionately.

"If the tropics are the engine of global diversity, then driving tropical populations into extinction will have a global effect by cutting off the primary source of new taxa for all latitudes" D. Jablonski, 2008

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