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OPINION ARTICLE

The "Hyper-Visible World" hypothesis for the dazzling colours of coral reef fish [version 1; peer review: 1 approved with reservations]

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Abstract

No evolutionary explanation for the striking colouration of coral reef fish has been established to date. Here I present the "Hyper-Visible World" hypothesis, which proposes that coral reef habitats impose special conditions on the evolution of body-colour communication for mobile fish – that is, fish that roam across coral reef formations. The special conditions are: 1) the high clarity of water during daylight hours, and 2) the unpredictable pattern/ visual complexity of the coral habitat itself. The hypothesis suggests that, in a signal transmission framework, the visual exposure (signal) of mobile fish cannot be effectively reduced so as to make a difference to predator-prey interactions. This negates the possibility of effective colour-based camouflage. In contrast, the selective pressures that usually come secondary to camouflage (such as sexual, aposematic or territorial display) benefit from these same conditions, driving the evolution of the colour patterns in this environment – the conspicuousness and dazzling colour diversity that we commonly associate with coral reef fish.

Keywords

coral reefs, fish, colours, camouflage, signal-transmission, evolution, conspicuousness

Open Peer Review

Approval Status

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version 1 12 May 2015	view		

1. **Brian Langerhans**, North Carolina State University, Raleigh, USA
2. **Theodore Stankowich**, California State University, Long Beach, USA
3. **Brett Seymoure**, Colorado State University, Fort Collins, USA

Any reports and responses or comments on the article can be found at the end of the article.

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Introduction

Being able to hide in plain sight is a major selective pressure for both prey and predator species^{1,2}. Traits increasing the ability of individuals to camouflage in the environment have likely been under strong selection since vision emerged, having guided to a great extent the evolution of visual displays in the animal world. It is in this context that the dazzling colouration of fish inhabiting coral reefs and other tropical bodies of water has puzzled scientists since the formulation of natural selection theory³⁻⁹. This flamboyance of colour patterns seems not only to disregard any pressure for blending in with the environment, but in fact suggests the opposite purpose: to make an individual stand out as much as possible, competing for attention.

Alfred Russel Wallace, co-proponent of the natural selection theory, put forward a hypothesis that relied instead on the existence of a camouflage purpose of those colours and patterns, whereby *“brilliantly-coloured fishes from warm seas are many of them well concealed when surrounded by the brilliant sea-weeds, corals, sea-anemones, and other marine animals, which make the sea-bottom sometimes resemble a fantastic flower-garden”*³. Even though camouflage may also work by disrupting, or breaking up, contrasting patterns that can make a prey/predator easily recognizable^{1,10}, the fact is that most fish inhabiting coral reefs can be easily seen to the point that, in fact, 1973 Nobel Prize winner, Konrad Lorenz, proposed a hypothesis which is based in a total denial of disguise function in that context. Instead, Lorenz suggested these dazzling colour patterns would be a robust means of species-recognition in the highly diverse and multi-niche environment of coral reefs, where such distinct signalling patterns would be needed to prevent aggression among non-competitor species⁴. However, many of the colourful fish found in corals are not necessarily aggressive or territorial¹¹. Therefore, to date no hypothesis has in fact proven resilient to existing empirical data and this evolutionary puzzle remains at large⁴⁻⁹.

The hypothesis

Here I present the “Hyper-Visible World” hypothesis, which proposes that coral reef habitats impose special conditions on the evolution of body-colour communication for mobile fish – that is, fish that roam across coral reef formations-leading to an impossibility of the use of camouflage while promoting the selective forces that benefit from conspicuousness. The special conditions are: 1) the high clarity of water during daylight hours, and 2) the unpredictable pattern/visual complexity of the coral habitat itself. These conditions negate the possibility of camouflage for most mobile animals in such habitats (some species can change the body coloration in real time as they roam over different backgrounds, but this is a highly sophisticated and demanding feature restricted to a few species like some octopuses). Because signalling patterns evolve as a trade-off between predation and other selective pressures¹², when predation under varying degrees of visual conspicuousness is similarly efficient, other selective pressures for communication that benefit from conspicuousness (e.g. sexual or warning signalling) can evolve without the constraints imposed by the need for camouflage.

The hypothesis may be also understood within a signal transmission framework, where the visual conspicuousness of an individual

represents the signal. As such, in coral reefs, the intensity of the signal conveyed by mobile fish cannot be reduced as to lessen predatory pressures. The exceptionally good environment for signal transmission (clear waters) and the unpredictability of the “background noise” (diverse coral reef) for a dislocating individual, makes the reduction of signal-to-noise ratio exceptionally difficult. In fact, the Hyper-Visible World hypothesis lays out a specific and falsifiable (*sensu* Popper¹³) prediction: other traits being equal, roaming fish with any degree of visual prominence will endure equivalent predatory pressure (or success) in coral reefs, but not when swimming against a predictable background.

It is important to highlight spatiotemporal dynamics¹⁴ involved in this theory: the degree of mobility of fish in the geography of coral reef habitats plays a pivotal role in the predictability of the background, and hence in the evolution of camouflage. If a fish roams against a variety of backdrops, the likelihood of effective camouflage is close to null. If, on the other hand, a fish spends most of his time in one location, natural selection will favour pigmentation and morphologies that match that predictable substrate (be it a coral species, type of rock or sand). Interestingly, because visual acuity is so high in the transparent waters of coral reefs, the need to “deceive with perfection” is also exceptionally high, leading to the “hyper-naturalism” found in the camouflage patterns of fish like pygmy sea horse or anglerfish, which is more typical of terrestrial environments (where visibility is also usually excellent) than of other marine habitats.

Selective pressures driving the evolution of colour patterns (but that usually come secondary to camouflage) benefit precisely from those conditions that are adverse to concealment. Those selective pressures range from hostile to friendly signalling. Among conspecifics, for example, signals range from those communicating willingness to engage in dispute over resources to stressing bonding forces for school formation and sexual attraction. In interspecific interactions, signals may range from warnings of retaliatory weaponry (e.g. aposematism by poisonous fishes) to the marketing of services (e.g. special colours and approaching behaviours of cleaner fishes^{4,15}). However, while selective pressures for conspicuousness are favoured by the transparency of the medium, they are hampered by the complex and colour-rich background of the coral reef - hence the pressure for the “hyper-unnatural” (i.e. not often found in nature) colour patterns of many reef fish.

Although the Hyper-Visible World hypothesis relies on the notion that camouflage in coral reefs is not an option for many mobile species, selection for camouflage can be also relaxed in other contexts. One such case is that of non-predatory species endowed with effective defence mechanisms against predators. The hummingbirds’ speed or the nut-cracking beaks of parrots probably did not evolve as defences against predation, but are effective in that sense, freeing those animals from the need to visually blend in with their surroundings. Similarly to what is found in coral reefs, other evolutionary pressures for colouration could then take over.

A Hyper-Visible World, we speculate, can also help drive biological diversity. Signalling in high visual resolution can promote the genesis of new species through sensory-drive^{12,16}, a process whereby

subtle changes in either colour patterns or in sensory/cognitive biases for attraction to those patterns can lead to the reproductive isolation of part of a population. In this sense, the high resolution of signals coupled with the high productivity of coral reefs might account for the high rates of sympatric speciation observed in these habitats.

Justin Marshall, a specialist in the study of colour vision observed that it “*is almost inconceivable for only one evolutionary force to be behind the colours of such a diverse assemblage*”⁶. Indeed, should the Hyper-Visible World hypothesis prove accurate, it is paradoxically the very elimination of only one evolutionary force (camouflage) that sets the artistic boldness of several other pressures free for drawing the magnificent mosaic of colours and shapes found in these marine ecological wonders.

Competing interests

No competing interests were disclosed.

Grant information

The author(s) declared that no grants were involved in supporting this work.

Acknowledgments

I am grateful to Gil Rosenthal, for his comments on an earlier version on this paper, and to Cynthia Schuck-Paim, Nigel Pearn and Veronique Vicera for their comments and editorial content revisions. This paper is dedicated to the dear friends of the memorable 2014 sailing trip, the occasion when I formulated this theory while diving in the outstanding Caribbean waters.

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Brian Langerhans

Department of Biological Sciences, North Carolina State University, Raleigh, NC, USA

The paper offers a hypothesis concerning the "striking colouration of coral reef fish." The idea is that coral reef fish roam across complex/unpredictable background colors and patterns within a transmission environment which permits highly effective perception of a range of light (color) to a variety of organisms capable of receiving and processing the respective light waves (during daytime). The argument rests on a number of assumptions, leading to the conclusion that selection will not favor camouflage in such an environment, and thus selection favoring conspicuous signaling is largely unconstrained. I think there is a useful hypothesis described here, which points out several testable ideas. However, I think each key assumption should be more directly addressed in the paper. Otherwise, one can see that the entire "Hyper-Visible World Hypothesis" could come crumbling down if those assumptions are wrong.

The first assumption needs more support: that coral reef fishes actually exhibit significantly higher color conspicuity or diversity than most other organismal assemblages. The entire hypothesis rests on this premise. Have studies tested whether coral reef fish actually exhibit such remarkable color patterns compared to other assemblages throughout the world? I agree that they surely must represent one of the more colorful, conspicuous, and diverse assemblages--but I'm not sure they are so remarkable that they deserve a special hypothesis unto themselves. It'd be nice to see some support for this premise. If this premise were untrue, then there is no need for a unique explanation for the colors of coral reef fishes.

The next assumption is that coral reefs provide a background of complex and unpredictable colors. I recall some studies showing low diversity of color during daytime and under ambient light for coral reefs. The author suggests that reefs are extremely colorful and complex, but I'd like to see some support for this. I agree they do seem fairly colorful and complex to us humans, but I can actually think of a number of other environments which seem pretty colorful and complex as well. What have previous studies found regarding the actual background colors of reefs? Are they really that complex and unpredictable from the perspective of a predator? Or is the background mostly blue/green/brown?

The next assumption is that coral reef waters actually are "hyper visible." That is, do these waters provide a transmission environment for which an especially wide range of color signals are accurately and efficiently transmitted? The waters are generally quite clear (low turbidity, high visibility), but air actually provides more effective transmission of light across all the relevant wavelengths. It seems to me that these waters actually truncate the red/yellow/orange wavelengths (to various extents), and thus are not "hyper visible" in that sense. Perhaps some further discussion of this point is warranted, as I'm not sure in what sense the waters are actually hyper-visible, but rather the organisms within the environment are highly visible due to a combination of water clarity and colors.

The next assumption is that many resident organisms have well developed color vision. This is actually quite well supported by the literature, although it'd be nice for this paper to explicitly support this assumption as well.

The final assumption is really more of a prediction: that selection will not favor crypticity in such an environment, and thus we should not see cryptic organisms (but rather the evolution of conspicuous colors, which is the heart of the hypothesis). I doubt this is as universal as suggested in this paper. There are actually many examples of cryptic organisms inhabiting coral reefs (at least during a substantial part of their lives), including many fishes. Not only are there many coral reef fishes which are quite cryptic (e.g., peacock and leopard flounders, scorpionfish, frogfish, many blennies and gobies, trumpetfish...), but also many exhibit some cryptic components, such as countershading and disruptive coloration (including false eyes for misdirection). The prevalence of countershading seems to suggest that some crypticity has long continued to be advantageous in reef environments, although highly conspicuous signals are additionally advantageous. Moreover, the author's hypothesis that crypticity should primarily be favored in relatively sessile fishes could be directly tested (this could be mentioned in the paper)--and if the author could support this contention, that would be great (that most known examples of camouflage in reef fishes are in relatively stationary species).

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Author Response 07 Mar 2016

Wladimir Alonso, Origem Scientifica, São Paulo, Brazil

Dear Brian,

Thank you very much for your review, relevant comments and for allowing me the opportunity to provide more evidence and clarify the assumptions on which my proposed hypothesis rests on. Your name, together with others –who provided me with feedback, will be included in the acknowledgment section of this manuscript, in recognition of your time and expert feedback. In totality, the constructive criticism and discussion this paper has generated has helped me realize that I should also somehow present these ideas in a systematized and slightly more organized format. The current version therefore provides a

framework that more formally addresses the topic of the conspicuous coloration of certain animal species, like macaws and hummingbirds, which were just included as an additional note in previous version. Without adding too much extra content, I managed to create a couple of new sections including a new designation - "the carefree world" in addition to a figure that both integrates and summarizes those ideas.

Below I have addressed the assumptions you specifically mentioned and that would need further support and clarification:

#1 "coral reef fishes actually exhibit significantly higher color conspicuity or diversity than most other organismal assemblages. *The entire hypothesis rests on this premise. Have studies tested whether coral reef fish actually exhibit such remarkable color patterns compared to other assemblages throughout the world?"*

WJA Reply:

I haven't succeeded in finding a reference of a study that quantifies that coral reef fish exhibit higher colour conspicuity or diversity than most other organismal assemblages. It seems that it is a given in the field, and scientists express in sorts of ways like this: "There is in all the world, no other biotope which has produced, in so short a time or, which means the same thing, in so closely allied groups of animals, an equal number of extremely specialized forms" (1) or "A coral reef is perhaps the most colorful of all the world's ecosystems. During the day it throngs with multicoloured fish and invertebrates" and "there is nowhere on earth where one can find so many colourful animals packed into such small space" (2) Nevertheless, despite perhaps not being quantified in the way we would like it, this is an observation that is widely supported and the one which all the hypothesis mentioned in this text since Wallace's one, try to find an answer.

Furthermore, allow me to also address your remark that *"I agree that they surely must represent one of the more colorful, conspicuous, and diverse assemblages--but I'm not sure they are so remarkable that they deserve a special hypothesis unto themselves. It'd be nice to see some support for this premise. If this premise were untrue, then there is no need for a unique explanation for the colors of coral reef fishes"*.

WJA Reply: As surprising as it may seem, the abundance of bright and colourful fish in coral reef, that so markedly stands out visually, -where we should expect to witness animals trying to blend into the surroundings, so they do not become "an obvious meal"(3) is still an open question and the subject itself, has given rise to several studies and conjectures to address it (as shown in the introduction of the paper). I do agree with you on your point that any hypothesis looking at it should aim for a broader scope, as mechanisms in nature rarely are specific to only one circumstance. I just found a passage in Cott's 1940 book that can be considered another example of a "hyper-visible world," which I am including as an opening citation in the "Hyper-visible world" section of the new version

#2 " coral reefs provide a background of complex and unpredictable colors. *I recall some studies showing low diversity of color during daytime and under ambient light for coral reefs. The author suggests that reefs are extremely colorful and complex, but I'd like to see some support*

for this. I agree they do seem fairly colorful and complex to us humans, but I can actually think of a number of other environments which seem pretty colorful and complex as well. What have previous studies found regarding the actual background colors of reefs? Are they really that complex and unpredictable from the perspective of a predator? Or is the background mostly blue/green/brown?

WJA Reply: Matz et al (4) used spectrometry data and visual system modelling to answer the question posed in the title of their article "Are Corals Colourful?" This article attempted to answer such questions from the perspective of the fish and found that "*Some GFP-like proteins, most notably fluorescent greens and nonfluorescent chromoproteins, indeed generate intense color signals.*" They go on to explain that "*fluorescent proteins might also make corals appear less colorful to fish, counterbalancing the effect of absorption by the photosynthetic pigments of the endosymbiotic algae, which might be a form of protection against herbivores.*" But as they even discuss at the end, "*It is tempting to speculate that the evolution of diverse coral colors in early Mesozoic (3) might have prompted the specialization of the fish visual systems in the process of adaptation to the environment, eventually leading to appearance of very unusual color signaling displayed by present-day reef fishes.*" Therefore, I believe it is a sound assumption that coral reefs are not only perceived as colourful to humans but are also perceived as such by (often chromatically more sophisticated eyes (5)) their aquatic inhabitants as well. I modified the text accordingly to include these references and a summary of those considerations.

In any case, please note that if colour vision were not found in predatory interactions within the context of the hypothesis presented, this would not be an issue for the hypothesis since mobile fish in the "hyper-visible world" cannot hide, regardless of their colour, meaning predators/prey also need not use colour vision (again, for their interactions). This is also valid in the "carefree world" scenario, where, if a predator cannot risk hunting a dazzlingly colourful macaw, why would evolution bother providing that predator with the visual capabilities customized to detect a macaw?

3 "**coral reef waters actually are "hyper visible."** That is, do these waters provide a transmission environment for which an especially wide range of color signals are accurately and efficiently transmitted? The waters are generally quite clear (low turbidity, high visibility), but air actually provides more effective transmission of light across all the relevant wavelengths. It seems to me that these waters actually truncate the red/yellow/orange wavelengths (to various extents), and thus are not "hyper visible" in that sense. Perhaps some further discussion of this point is warranted, as I'm not sure in what sense the waters are actually hyper-visible, but rather the organisms within the environment are highly visible due to a combination of water clarity and colors"

WJA Reply: Coral reefs are usually found in shallow, clear tropical waters where the spectral attenuation of light by transmission medium (water) has not yet been severe. (2). In fact, only very little of the downwelling light, while the horizontal light is "less intense, narrower and shifted to the blue" (5)(6). Many fish can see even UV light, so they are able to perceive an even greater variety of colours than we do. You are correct in pointing out (and I do also points this out in the paper) that the excellent visibility of coral reefs habitats are nonetheless inferior to most of the terrestrial. But do note that the "hyper-visible world" is a

way to express the impossibility of matching a background pattern in certain conditions and that difficulty is imposed not only because of the good transparency and luminosity of the medium, but equally important is the unpredictability of the background to be matched. Terrestrial environments (as discussed in the first answer) seem to be more predictable (but, again, please see the first new paragraph of the Hyper-visible World section quoting an interesting parallel explanation in Cott's 1940 book) . While this is true for visual signals, perhaps this is not the case for acoustic and olfactory signals (which is why I added that small discussion at the end of the paper in the current version.

4 "**many resident organisms have well developed color vision. This is actually quite well supported by the literature, although it'd be nice for this paper to explicitly support this assumption as well**"

WJA Reply: As suggested, I added Bennet et al review (7), which explains how vision in those environments can be more sophisticated than ours (including UV vision and a higher number of different photoreceptors, which are common in marine species.

5 "*The final assumption is really more of a prediction: that **selection will not favor crypticity in such an environment, and thus we should not see cryptic organisms (but rather the evolution of conspicuous colors, which is the heart of the hypothesis)**. I doubt this is as universal as suggested in this paper. There are actually many examples of cryptic organisms inhabiting coral reefs (at least during a substantial part of their lives), including many fishes. Not only are there many coral reef fishes which are quite cryptic (e.g., peacock and leopard flounders, scorpionfish, frogfish, many blennies and gobies, trumpetfish...), but also many exhibit some cryptic components, such as countershading and disruptive coloration (including false eyes for misdirection).*"

WJA Reply: You spotted an error that was also pointed out by a comment from Benjamin Geffroy; that is, I incorrectly used the expression "will" where it should read "can." I have since corrected it in the revised version. But please do note that this hypothesis stresses the importance of the "mobile" (i.e. spatio-temporal) feature for making it very difficult for organisms to evolutionary develop a pattern that can provide some concealment against predators or preys. I hope that the new figure added to the paper helps to further clarify the circumstances where coral reefs can indeed support camouflage (which basically occurs when animals are loyal to one specific background during daylight hours).

#6 "*The prevalence of countershading seems to suggest that some crypticity has long continued to be advantageous in reef environments, although highly conspicuous signals are additionally advantageous. Moreover, the author's hypothesis that crypticity should primarily be favored in relatively sessile fishes could be directly tested (this could be mentioned in the paper)--and if the author could support this contention, that would be great (that most known examples of camouflage in reef fishes are in relatively stationary species)*".

WJA Reply: Indeed, countershading, disruptive camouflage and other forms of concealment are not negated among diurnal mobile fish in coral reefs. The extraordinary abundance of life forms and solutions to the constant predator/prey interactions certainly include these mechanisms (and possibly others we haven't described yet). Nevertheless, the question

remains of why there are so many fish that are so easily detectable, even for humans. Furthermore, this species is only a visitor in the described environments and the reason for why senses which do not define the need to see those species - is not covered by those explanations. It has been shown that fish can develop visual capabilities that are far better than ours - if doing so would provide them with the ability to escape from or catch those colourful fish, it would be surprising that they would not use/develop those very capabilities.

Thank you once again for your appreciated input.

Best,
Wladimir

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Competing Interests: No competing interests were disclosed.

Comments on this article

Version 1

Author Response 07 Mar 2016

Wladimir Alonso, Origem Scientifica, São Paulo, Brazil

Dear Ben,

Thank you very much for your encouraging note and your very relevant feedback.

Below are my responses to your comments:

B#1 "I've been reading your piece with a particular attention. I really liked your proposition. I just identified one possible caveat, that you should take into account from my point of view. As you underlined: "If, on the other hand, a fish spends most of his time in one location, natural selection will favour pigmentation and morphologies that match that predictable substrate (be it a coral species, type of rock or sand)." However there are some examples of fish living in very high degree of vicinity with their home habitat that display very different colour pattern to their predictable substrate."

Thank you for pointing this out. You are indeed correct regarding my imprecision in the sentence you have referenced. I am changing the word "will" to "can" in the text to emphasize that the conditions allow for the possibility of camouflage, rather than an "imposition" for camouflage. But, of course, as you accurately pointed out, fish, particularly clownfish, don't follow this "rule." This is exactly the case with macaws and hummingbirds, which I did cite, and in which the circumstance is not that the organism cannot camouflage, but it does not *need* to camouflage. It has the protection of sea anemones, so why bother when it can utilize the canvas of the body for other purposes.

I also added a figure in this version that attempts to highlight the difference between these two important circumstances which are unfavourable to camouflage mechanisms ("adverse conditions for camouflage" found among roaming fish in coral reefs and "no need for camouflage" found among macaws and hummingbirds)

So, going back to your clownfish example, because in this particular case, they are so well shielded against predation by their biological alliance with poisonous anemone, their striking coloration is a product of residing the "carefree world" region above, rather than the "hyper-visible world." The clownfish develop conspicuousness not out of impossibility (the background where it spends most of its time -the anemone- is quite predictable), but out of disdain for camouflage. This is a descriptive example I hadn't thought about previously, and so I am adding it to the edited version.

As for your comments observed during your own experience in Fernando de Noronha (lucky you!), I would say that, despite the coral reefs not being as colourful as in other places, the "hyper-visible" conditions are still present: the water is very transparent and the background is still very unpredictable for those species that roam near the rocks/corals, so therefore, camouflage is not an option for them. You are indeed correct in your argument that comparative studies need to take into account all conditions in these different habitats (micro and macro) and can test this (as well as alternative) theories.

Thanks once again for your much appreciated input.

Best,

Wladimir

Competing Interests: No competing interests were disclosed.

Reader Comment 01 Jul 2015

Benjamin Geffroy, Laboratoire de Physiologie et Génomique des Poissons, Campus Beaulieu, France

Dear Wladimir,

I've been reading your piece with a particular attention. I really liked your proposition. I just identified one possible caveat, that you should take into account from my point of view. As you underlined :

"If, on the other hand, a fish spends most of his time in one location, natural selection will favour pigmentation and morphologies that match that predictable substrate (be it a coral species, type of rock or sand)."

However there are some examples of fish living in a very high degree of vicinity with their home habitat that display very different colour patterns to their predictable substrate. The species that directly comes to me are clownfish. While they display amazing colour, it is possible to well distinguish them from their home habitat (anemones). These fish spend about 95% of their time within or in close vicinity with anemone. There might also be other species that doesn't move so much, and I think you should definitely talk more about it to reinforce your argument. For clownfish, colour pattern attracting predators might not be so "costly" since they are protected by anemones. But it might not be so clear for other species and it would be worth developing your argument by discussing it. Another thing, I just had the opportunity to visit the incredible Fernando de Noronha island (that you might know), corals are not so colourful (compared to other places in the world) while many species display striking colours (Thalassoma noronhum comes to me, as well as many damselfish species) in praia sueste for instance. According to your hypothesis, the contrast between habitat and fish should be minimized, to reduce predation risk. As such we could expect that selection would act by selecting fish with lower pigmentation level over time in such places Endemic species might thus display a colourful pattern different to that of sister species from caribes for examples. There (in FN) you have a good place and some good examples to test your hypothesis

Good luck for the paper, and I await to see it published soon.

Best

Ben

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