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Influence of Climate Change on Obligatory Interactions in the Ecosystem: Predicting the Future

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Abstract

Obligatory interactions in the ecosystem are sensitive to climate fluctuations. The study of how mutualistic and parasitic associations which are obligatory for the partners, respond to past climate change especially in the Quaternary, would help deepen the understanding and provide clues to how ecosystems would respond to current and future climate changes. Data was obtained by searching through articles from different scientific databases spanning from 1990 to 2022. The focus was on decoupling of partners, changes of the distributional limits of partner species and response to sudden climate change by the interacting partner species. From this review, data on response of obligate interactions to past climate change is limited and all constraints should be removed to allow for sufficient and appropriate data. Efficient calibration of demographic events from genetic data coupled with use of suitable biological models; including enhanced number of models from the tropics to help resolve the difficulty of timing biological events may be the way forward.

Keywords: obligate; interactions; Quaternary; climate change; ecosystem:
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1. Introduction

Climate change is affecting ecosystems at multiple scales resulting in the emergent of new dynamics through shift in productivity and species interactions. Changes in the morphology and behaviour, phenology and range shifts are observed in individual species and populations (Weiskopf *et al*. 2020). Species respond individually to climate fluctuations, and species that do not co-occur may do so in the future. Again, species that occur-together may become increasingly decoupled. These changes in species interactions have enormous potential to alter community structure and composition and ultimately drive the dynamics of biodiversity. Climate fluctuations can cause shift in the timing of biological events which affect species and habitats in the ecosystem. The species will have to evolve to keep pace. Thus, the response of ecosystems to climate change is key in assessing evolution of life. These responses are better understood by analyzing the ecological relationships among organisms, and between organisms and the environment (Seifert *et al*. 2022; Sultan 2015). An organism`s interactions with its environment are fundamental to the survival of that organism and the functioning of the ecosystem (Weiskopf *et al*. 2020; Balter *et al.* 2019). The relationships among organisms, either interspecific or intraspecific are better understood by analyzing the proximate and ultimate levels to know traits that help an organism to survive in its niche (Fraser *et al*. 2021). Past climatic oscillations are of special importance in the understanding and interpretation of biotic changes in the past and for forecasting the biotic response to future climatic fluctuations.

Mutualism and parasitism are typical biotic interactions which can be obligatory. In obligatory interactions, at least one partner depends on the other. A mutualism is obligate when both species benefit from the relationship. Reciprocal benefits play a substantial role in promoting biodiversity by increasing species alliances, coexistences, diversity and stability (Hale *et al*. 2020). Parasitic interactions are beneficial for one species but detrimental to the other species. Parasitism has major impact on host growth, allometry and reproduction and therefore affect population dynamics by driving host evolutionary trajectories (Okamura *et al*. 2018; Walker *et al*. 2017). Mutualistic interactions provide insight into species co-existence, diversity and community robustness; and regulate species richness at different scales by modulating speciation (Bascompte 2019). Co-evolution that prevails in host-parasite interaction increases trait diversity within a community by facilitating co-existence among competing species (Betts *et al*. 2018; Papkou *et al*. 2016). These obligate interactions help maintain biodiversity in the ecosystem.

Global change has impacts on ecosystem form and function. Climate fluctuations have the potential to disrupt mutualistic and parasitic interactions by having direct negative impacts on one or both partners. The interacting partner species may respond individually to climate change however, they need each other for survival. Mutualistic and parasitic interactions are sensitive to climate fluctuations (Bascompte 2019). Thus, studying the responses of partners to sudden past climate changes will bring to fore changes that are presently occurring in the ecosystem and also help to predict future changes in the ecosystem. The current knowledge on the life histories of species and populations have largely been obtained from evidences provided by studies on paleontology (Bicknell *et al*. 2022; Kimura *et al*. 2021; Shamsabad *et al*. 2019) and genetic data of current populations (Childebayeva *et al*. 2022; Nieto-Blazquez *et al*. 2022; Okazaki *et al*. 2021; Marchi *et al*. 2021; Guo *et al*. 2016). Climate proxies are used to reconstruct past climate to build up data. These records are integrated with observations from modern climate and then modelled to infer the past as well as predict the future climatic conditions (Isbell *et al*. 2021). Around the same period, studies on reconstruction of past vegetation using pollen records intensified (Sugita 2007). The outcomes from these two researches allow for assessment of the intensity of past climate changes and related responses of ecosystems (Echeverria *et al*. 2022; Liu *et al*. 2021; Carvalho *et al*. 2019).

Milankovitch cycles account for many climatic fluctuations over long time period (Caccamo & Magazu 2021; Puetz *et al*. 2016). These cycles have occurred at different intensities and time scales ranging from ten thousand years to over a hundred thousand years (Lohmann *et al*. 2020), and have driven evolutionary changes in species and populations (Trinder *et al*. 2020). Tectonic organizations arise from processes such as redistribution of continents, formation of land bridges etc. to provide a moderate environmental pressure that stimulates population to adapt and evolve (Couvreur *et al*. 2021). A combination of Milankovitch cycles and tectonic organization is considered a major driving force of evolution influencing biodiversity and interspecific interactions (mutualism and parasitism) in the ecosystem (Xu *et al*. 2021; Gorter *et al*. 2020).

Various categories of the effects of past climate change on symbiotic interactions have been documented. These include disrupting the match between partners and the environment; reducing adaptability; driving ungulate population dynamics; enhancing or reducing fitness of partners; decoupling of partners (fragmentation); shifts in outcomes of existing partnerships (range shift); formation of new partnerships; and extinctions (Bascompte 2019). This study assesses how the effects of extinction of partners, decoupling of partners and changes of the distribution limits of partner species are expected to have influenced and shaped the evolutionary history of mutualistic and parasitic interactions during the Quaternary period. The Quaternary has been described as an important time for genetic diversification and speciation, since the period fostered the isolation of populations and in some instances, allopatric speciation.

The predicted responses of the populations in obligatory interactions are presented and illustrated with examples from literature. These will help understand how the partners are likely to respond under future changing climate conditions.

2. Materials and methods

This research is structured by a critical literature review, which was conducted to identify the effect of past climate change on behaviour and adaptation of species involved in obligate mutualism and parasitism. The review started with searching for articles from different databases (Scopus, Web of Science, PubMed, Academic Research, Google Scholar, JSTOR, Directory of Open Access Journals etc.) for review spanning from 1990 to 2022. The articles were filtered using the following keywords: Quaternary, Climate change, Obligate mutualism and parasitism; response, decoupling, distribution limit, and adaptation. The search for literature was finalized after getting to a point where new information was generally not available. The texts of the selected literature were screened to ensure the relevance of the content in terms of the inclusion criteria - the articles must be original, peer-reviewed, empirically researched using qualitative and quantitative approaches and written in the English language. A screening of the abstracts helped to discard articles which do not satisfy the basic requirements. A total of 88 peer-reviewed articles related to influence of climate change on obligate interactions (mutualistic and parasitic) were used for the study.

3. Results and discussion

3.1 Decoupling of partners

Landscape heterogeneity may allow persistence of species and populations throughout climate fluctuations (Bisbing *et al*. 2018; Oliver *et al*. 2010). Climate change induces changes in precipitation and temperature which cause spatial heterogeneity. Spatial heterogeneity appears to provide means by which species and populations are maintained (Willrich *et al*. 2019) due to the presence of specialized microclimates in which species find tolerable environments. Landscape heterogeneity may be represented by compositional or configurational heterogeneity where compositional heterogeneity supports communities with greater taxonomic diversity and configurational heterogeneity supporting communities that include vulnerable species (Seastedt & Oldfather 2021). Thus, individual specializations in behaviour are more pronounced in heterogeneous environment to maintain species and populations in particular microclimates (Trevail *et al*. 2021). In a high topographic heterogeneous landscape with sharp altitudinal variation, species can cope with climate cycles by shifting their altitudinal range distribution to be in other suitable microclimates at relatively shorter distances. New species arrivals can further mediate the impacts of fluctuation climate (Trevail *et al*. 2021; Seastedt & Oldfather 2021). In a study on topographic heterogeneity and patterns of vegetation response to climate change in USA, Bueno de Mesquita *et* *al*. (2018), indicated that elevational ranges of vegetation types have changed in a heterogeneous mountainous landscape in response to climate fluctuation. Trees and shrubs colonized Tundra, and only shrubs expanded their elevational range. Each vegetation type had a unique microclimate best predicting its establishment in new areas. Vegetational change in response to past climate fluctuations in tropical Africa showed that a move to warmer and wetter conditions (heterogeneous condition) in the past resulted in a range distribution of mostly woody plants up to 500 km north of its present location. (Willis *et al*. 2013). Spatial heterogeneity in climate fluctuation limits species dispersal capabilities and adaptive potential. In hotter areas, species that require moist conditions are restricted to riversides and in cooler regions, species that need warm conditions are found in sun-exposed areas (Senner *et al*. 2018).

The role of refugia in the persistence of ecosystems and communities has been validated in the temperate and boreal regions (Morelli *et al.* 2020; da Rocha & Kaefel 2019). The glacial episodes of the Quaternary have shaped the present-day distribution of extant biota. During the glacial period, forest was restricted to favourable climatic areas called forest refugia; and after this period when the climate warmed, the forest refugia expanded to new areas. Thus, areas relatively buffered from past climate change over time enabled the persistence of temperate and boreal ecosystems (Stralberg *et al*. 2020; Michalak *et al*. 2018). The strength of refugia is a combination of temporal persistence and the shape of anticipated response to climate change and disturbance (Zajac *et al*. 2020). Understanding such refugia is critical in predicting species distribution and survival as the earth heads into another period of climate change (Wen *et al*. 2017).

In the tropics, the role of forest refugia in predicting the life history and diversification of biota has had difficulties and challenges. The forest refugia theory in the tropics has no uniformity in interpretation and there is no palynological evidence to support the theory (Rossetto & Koooynan 2021; Sophie *et al*. 2019). According to Murienne *et al*. (2013), refugia may have acted as “museums” during the past climate fluctuation period in conserving ancient diversity rather than being source of generating diversity. The forest refugia hypothesis which was proposed in Amazonia (Brazil) sought to explain how response of biota to past climate change provide understanding of the mechanisms behind the diversification processes in the Amazon-forest (da Rocha & Kaefer 2019). However, critics argue that the forest refugia hypothesis alone cannot explain the origin and maintenance of the Amazon diversity and may be, it was not the dominant mechanism of species differentiation. Moreover, the existence of refugia for a whole ecosystem, and the palynological evidence concerning forest fragmentation during the last Glacial Maximum and Holocene periods have been questioned amidst different interpretations (da Rocha & Kaefel 2019; Bush & Oliveira 2006). In the Central African rainforest, the Pleistocene refugia hypothesis has shaped the population structure, providing support for their role as potential engines of diversification (Ntie *et al*. 2017; Murienne *et al*. 2013). However, the concept of “Universality of potential refugia” has faced challenges as the delimitation of “Universal rainforest refugia” remains difficult to establish.

Notwithstanding the difficulties and challenges associated with the theory of refugia, researchers generally agree that many species have maintained viable populations in favourable areas throughout past climate fluctuations.

Refugia may have been different for partner species in symbiotic mutualism and parasitism interactions (Hale *et al*. 2020; Mies *et al*. 2017). The effect of past climate fluctuation is stronger in these interactions as the two partners for each interaction, are completely interdependent for survival and reproduction (Pauli *et al*. 2022). The partner species in symbiotic mutualism and parasitism may have different life-history traits (Nakazawa & Katayama 2020); and population isolation may affect the partners differently (Hernandez-Yanez *et al*. 2022; De Vrient *et al*. 2017). Symbiotic interactions are formed by the long-term intimate association of the host species (plant/animal) and microorganisms (Nadarajah & Abdul Rahman 2021). The host has a longer generation time than the symbiont (microorganism) which has a relatively good dispersal capacity (Wisselink *et al*. 2020). Though the host and symbiont may have a common history, they may show different phylogeographic patterns because of the differences in life-history traits (Coryell *et al*. 2018; Schiebelhut & Dawson 2018). It is predicted that the host (plant/animal) should display phylogeographic patterns consistent with documented patterns of organisms of similar size. The symbiont (microorganism) is likely to have phylogeographic pattern different from that of the host or no pattern is formed. The above interactions between the host (plant/animal) and the symbiont (microorganism) may show incongruous traces of the past.

In symbiotic interactions, partner species with shorter generation time and higher mutation tendencies, usually have a stronger differentiation; and this may lead to formation of local variants (Weller & Wu 2015). Thus, decoupling (fragmentation) of partners in symbiotic mutualism and parasitism may lead to speciation in only one of the partners or in both partners but at different rates. This indicates that pattern of speciation may be linked to past climate change. Climatic oscillations appear to have played a role in promoting speciation of two langur species (Li *et al*. 2022). The researchers showed that climate change impacted on the divergence of two langur species, *Trachypithecus francoisi* and *Trachypithecus leucocephalus* by causing cessation of gene flow during the Last Glacial Maximum (LGM, 26.5-19 Kya) which promoted speciation of the two species (Li *et al*. 2022).

Past climate change has had differential impacts on symbiotic mutualism and parasitic (obligatory) interactions. To have insight into this, species-interactions with partners having different life -history traits and one of the partners possibly having speciation after population decoupling have been used. This allows for the understanding of the consequences of decoupling of partners on the population genetics of interacting-species. The interaction between fig plant and its pollinating fig wasp shows obligate mutualism between plant and its gall-inducing insect. Most mutualisms involving galling insects are specific and mostly exhibit co-diversification, co-speciation and co-evolution (Wang *et al*. 2019). In this interaction, pollination of the fig plant depends on specific insect (wasps) which feed on seeds of the plant (Borges 2021). The female fig wasps deposit eggs and develop their progeny in galled female flowers while the fig wasps pollinate female flowers (Juaharlina *et al*. 2022). The relationship between yucca and yucca moth is an example of the importance of obligate interaction in specialization and diversification. Yucca plant (eg. *Yucca aloifolia*) and yucca moth (eg. *Tegeticulla* sp.) exhibit obligate mutualism where the moth pollinates yucca flowers and larvae of moth feed on yucca seeds (Arteaga *et al*. 2020). In an ant-plant protective mutualism, the plant provides food and habitat for the ant and the ant pollinates the plant. The seeds of the plant have specialized structures called elaiosomes that ants like to eat. The presence of the ant increased plant reproductive output by 14% and reduced herbivory by 62% (Trager *et al*. 2010).

In an antagonistic interaction between plant (*Arum maculatum*) and two psychodid insects (*Psychoda phalaenoides* and *Psycha grisescens*), the insects pollinate the plant. This antagonistic interaction is obligatory for only one of the partners. The genetic structures of the interacting species show that the plant and the two insects show phylogeographic patterns which are not congruent indicating that they may have different life-history traits. Though the interacting species may be from the same refugia, the plant and insect lineages do not share the same glacial and inter-glacial histories (Espindola & Alvarez 2011). The phylogeographic pattern of *Arum maculatum* is consistent with that obtained from glacial refugia during recolonization of Europe. The incongruous phylogeographic pattern between plant and the insects may be due to the extensive dispersal and gene flow of the insects influencing their life histories, and the insects may have been maintained independently from the plant. In another antagonistic obligate interaction between Western North American chipmunks (host) and two

distantly related species of parasitic pinworms, there were signals of host-associated divergence in both parasitic species (Bell *et al*. 2018). Though the two parasites may have experienced similar past climatic fluctuations, their diversification processes were associated with differences in the initiation of their association with the host. There were shallower phylogenetic structure variations between the two parasites. The parasites, though may have experienced similar past climatic changes, showed partially congruent phylogeographic patterns. The two parasitic lineages may have partially shared the same glacial and post-glacial histories.

Reciprocally obligatory interaction with vertical transmission can be found in the associations between aphids and bacteria; and among ants, bacterial symbionts and fungal cultivars. Aphids (*Brachycaudis* sp.) harbour an obligatory symbiont bacterium (*Buchnera aphidicola*), providing essential amino acids not supplied by their diet (Figure 1). Investigations indicate that the bacterium is transmitted vertically and has “co-speciated” with the host (aphid). This “co-speciation” phenomenon has shown that *buchnera aphidicola* (bacterium) has diversified into independently evolving entities, each specific to a phylogenetic *Brachycaudis* species (Chen *et al*. 2017; Jousselin *et al*. 2009). Both the aphid and the bacterium show congruent phylogeographic patterns. This may be due to their similar life-history traits. In the next example, Fungus-growing ants (*Trachymyrmex septentrionalis*) have evolved close relationship with antibiotic-producing bacterial symbiont (*Pseudonocardia* sp.). Workers of the fungus-growing ant host the *Pseudonocardia* bacteria on their cuticle (Green & Klesson 2022). The ants provide nutrient to the bacterial symbiont and help cultivate basidiomycete fungi in the garden. *Pseudonocardia* bacteria produce secondary metabolite to protect the ants and fungal mutualist from pathogens such as *Escovopsis* sp. which attack the ants` cultivated fungi and the ants (Christopher *et al*. 2021; Goldstein & Klassen 2020; Batey *et al*. 2020). In the garden, *Pseudonocardia* sp. and fungal cultivar are transmitted by the ant (queen) vertically (Bartey *et al*. 2020; Goldstein & Klesson 2020). Although most of the fungus-growing ants are found in the tropical region (Solomon *et al*. 2019), *Trachymyrmex septentrionalis* is dominant in eastern United States of America (Senula *et al*. 2019). A possible explanation for this observation is that *T. septentrionalis* probably experienced population fragmentation (decoupling of partners) during the Quaternary glacial oscillations. Studies by Green & Klassen (2022) and Del-Castillo *et al*. (2017), indicate that there were two mostly allopatric western and eastern genetic groups of *T. septentrionalis* that probably diversified in the Pleistocene. Although the fungus-growing ant (T. septentrionalis), fungal cultivars and the bacteria (*Pseudonocardia* sp.) lived in obligatory symbiosis, past climatic fluctuations had different impacts on them. These were shown in their contrasting responses. Population genetic structures of *Pseudonocardia* sp. and fungal cultivars showed a pattern incongruent to that of the ant (*T. septentrionalis*). The observed pattern of differentiation could be due to the independent dispersal of symbiotic fungi and bacteria from the ant host. This may have resulted in different population dynamics due to the differences in life-history traits. In another example, studies on the obligatory interaction between the African ant plant *Vachellia drepanolobium* and three ants, *Crematogaster mimosae*, *Crematogaster nigriceps* and *Tetraponera penzigi* (Boyle *et al*. 2019) indicated that all three ants showed similar phylogeographic pattern (congruent). However, the phylogeographic pattern of the plant was different (not congruent) from all the three ants. The differential impact of past climate change on the partners could have resulted in differences in the phylogenetic patterns between *Vachellia drepanolobium* and the three ants.

Reciprocally obligatory interaction with horizontal transmission has been studied in two African rainforest species in Central Africa (Kokolo *et al*. 2019; Blatrix *et al*. 2017). *Barteria fistulosa* (plant) and *Tetraponera aethiops* (ant) lived in obligate interaction. The plant provides nesting cavities for the ant, and the ant protect the plant from herbivory. The seeds of the plant and founding queens of the ant disperse independently to form new associations at each generation (horizontal transmission). The trees and ants showed congruent phylogeographic pattern. However, further studies in the lower guinea region showed that there was a strong genetic differentiation (reproductive isolation) between plants of the northern and southern lower Guinea. This indicates independent speciation of partners which previously lived in specific and obligate interaction. This may have resulted from past climate cycles inducing forest contraction and expansion during the Quaternary (Pleistocene and Holocene) period and also contact with populations (plant species) from distinct refugia. *Tetraponera aethiops* (ant) species found in the northern and southern lower Guinea did not exhibit strong differentiation.

From the above illustrations, past climate fluctuations cause decoupling of interacting partners including that of obligate mutualistic and parasitic interactions. Climate cycles have differential impact on partners of obligate mutualistic and parasitic interactions and the genetic consequences are different between partners, though they might have shared the same refugia. The differential impact of past climate fluctuations on the partners who decouple is mainly due to differences in life history traits.

3.2 Changes of the distribution limits of partner species

Species generally respond to climate cycles by changing their distribution limits along altitudinal or latitudinal gradients (Wallingford & Sorte 2022; Couet *et al*. 2022). Climatic fluctuations alter ecological processes and partners of interaction are shifting their ranges to coincide with niche limits of the species (Wallingford & Sorte 2022; Lustenhouwer & Parker 2022; Shay *et al*. 2021). Interacting species face difficulties such as dispersal and establishment limitation in tracking climate change (Moran *et al*. 2022; Bosco *et al*. 2022). The extent of range shift in obligate mutualistic and parasitic interactions could be affected by intrinsic factors including tracking ability, dispersal capacity and habitat specificity of partner species (Yun *et al*. 2020). The dynamics of dispersal are likely to differ between partners and may influence their range shifts and eventually evolution of these interactions (Alzate & Onstein 2022). Synchronicity of range shift of partners of obligate mutualistic and parasitic interactions is needed for evolution of these interactions (Pauli *et al*. 2022; Alexander *et al*. 2022). In the host-parasite interactions, the range dynamics of parasites are relatively more constrained, and range shifts are mostly limited by the constrained partners (Scharsack *et al*. 2020; Aleuy & Kutz 2020). Generally, the range dynamics of a parasite is influenced by its life-history and range dynamics of the host (Aleuy & Kutz 2020) making the parasite relatively more constrained. As noted by Bellis *et al*. (2021), range shift of a host influences local adaption and even extinction of the parasite. Parasites have better diversity of life-history traits (Morand 2015) and relatively better dispersal abilities, and are more likely to track their host (Wells & Flynn 2022). The fastness and efficiency of parasites to respond to hosts range shifts differ from one system to the other (Wells & Flynn 2022). In obligatory mutualistic and parasitic interactions with partners having different life-history traits, a strong synchrony in range shifts is expected of the partners (for efficient coevolution). However, unpredictable outcomes are also expected in these interactions including novel co-occurrences among species leading to unseen biotic interactions such as exchange of parasites between previously isolated hosts.

Some examples have been put forward to illustrate the above expectations. During the Last Glacial Maximum, there was rapid northwards expansion of the tree *Fagus grandifolia* in North America (Denk & Grimm 2009; Fang & Lechowicz 2006). This expansion is not supported by the life-history traits of the tree since the tree has lower reproductive cycle and limited capacity to disperse seeds. Probably, low-density populations of the tree (*Fagus grandifolia*) persisted close to the ice margin. Moreover, the occurrence of cryptic refugia is recognized in North America and Europe (Zajac *et al*. 2020). The plant *Epifagus virginiana* is a specific parasite on *Fagus grandifolia* (Host) and it is expected that *Epifagus virginiana* tracked its host in the post-glacial colonization period (Tsai & Manos 2010). However, the genetic pattern of colonization of the parasite was different from that of the host. The parasite migration route was incongruent with that of host (parasite not tracking host at a point). Most probable explanation is that host (*Fagus grandifolia*) existed at low densities and the parasite (*Epifagus virginiana*) does not seem to establish population at low density (of host); and the parasite moved northwards only when the host established high density levels. In another example, the avian brood parasite lesser cuckoo (*Cuculus poliocephalus*) has twelve host (birds) species (Yun *et al*. 2020). Climate cycles during the Pleistocene may have caused distribution shift of the parasite on its twelve host species.

The parasite and hosts species showed similar phylogeographic pattern. Species distribution model system showed that the distribution shift of the parasite (*Cuculus poliocephalus*) on its 12 hosts species is likely to cause decrease in the geographical range of the parasite resulting in decrease amount of spatial overlap between parasite and host species. This indicates that range shift of the parasite may shrink due to host availability. Climate fluctuation may cause geographical shift of the parasite however, the parasite may be limited by spatial mismatch with host species. Considering the strong host specificity of the parasite, it is likely that the impact of climate change differs according to host races in the parasite. The range shrink of the parasites (*Cuculus poliocephalus*) limited the ability of parasites to track their hosts (Yun *et al.* 2020).

The gobiid fish (*Ctenogobiops feroculus*) and alpheid shrimp (*Alpheus djeddensis*) have obligatory mutualistic interaction in shallow coral reef lagoons in the Indo-Pacific region (Figure 2). The partner species independently cannot survive (Burns *et al.* 2019). During the Last Glacial Maximum, many of the present shallow lagoons suitable for habitation by mutualists did not exist. After the Glacial period, the sea level rose (above 100 m) to allow for the formation of coral reefs (Burns *et al.* 2019; Thacker *et al.* 2015). Both the gobiid fish and alpheid shrimp showed congruent phylogeographic pattern of colonization (recent eastward expansion). However, the phylogeographic pattern found in *C. feroculus* (gobiid fish) and *A. djeddensis* (alpheid shrimp) was not fully congruent with those found in six other lagoon fishes (Thacker *et al.* 2015). This probably indicate that similarity of the phylogeographic patterns exhibited by gobiid fish and alpheid shrimp was due to their obligate mutualistic interaction. In the next example, the yucca tree (*Yucca brevifolia*) and its pollinating moths (*Tegeticula synthetica* and *Tegeticula antithetica*) are engaged in obligate mutualism. The moths pollinate yucca tree flowers (Figure 3) and lay their eggs in the style, and the larvae of moths feed on portion of the developing seeds of the yucca plant (Cole *et al.* 2017). Two other moth species of the genus *Prodoxus* are considered to be parasitic on yucca plant (*Yucca brevifolia*) as they depend on the plant to complete their life cycles but do not pollinate the plant (Cole *et al.* 2017). Fossil records indicate that *Yucca brevifolia* was widespread during the late Pleistocene period and its range contracted at the beginning of Holocene period. Distribution models generally showed that the plant *Yucca brevifolia* did not experience range reduction during the glacial period but shifted its range northward and southward periodically (Cole *et al.* 2017; Cole *et al.* 2011). Notwithstanding the fact that during the late Pleistocene, the range shift of the plant (*Yucca brevifolia*) may not have been substantial, the five interacting species (yucca plant and four moth species) showed concerted population expansion. The probable explanation is that interdependent species respond to past climate changes at the same time (simultaneously) and the parasites closely tracked the population changes (range shift) of their host (Cole *et al.* 2017; Cole *et al.* 2011). In this present example, Epicephala moths (Gracillariidae) form obligatory mutualism with phyllanthaceae plant (*Breynia oblongifolia*). The moths pollinate the plant and they also depend on the female host plant flowers for oviposition sites (Figure 4) (Finch *et al.* 2021). Fossil records and distribution models indicate that moths synchronized their activities with that of the host (plant) and during the late Pleistocene period, there was synchrony of plant and pollinator (moths) life-history traits. The range shift of moths synchronizes with that of host plant suggesting that moth (pollinator) tracked the flowering plant. Both pollinator (moth) and host (plant) showed similar phylogeographic patterns (Finch *et al.* 2021) with the mutualist (moth) tracking the host.

In North America, the parasite *Parelaphostrongylus tenuis* develops into adults and reproduce inside a cervid host *Odocoileus virginianus* (reservoir host). Upon excretion from *O virginianus*, the larval stage of the parasite develops further inside gastropod host (intermediate host). The parasite is then transmitted to two other cervids, *Alces alces* and *Rangifer tarandus* (hosts) where the parasite develops into adult. *Alces alces* and *Rangifer tarandus* are considered as dead-end-hosts because the parasite does not successfully reproduce inside these hosts (Feldman *et al.* 2017; Upshall *et al.* 1987). It is expected that past climate fluctuations during the Holocene period may have influenced range shifts and distribution of these interacting species. For the host species (*Alces alces* or *Rangifer tarandus*), parasitism may occur in the part of its range that overlaps with a second host species (*Odocoileus virginianus*). The size of range overlap influences the level of host-parasite interaction. Species distribution modelling suggest that the range overlap between *Alces alces* and *Rangifer tarandus* and the parasite *Parelaphostrongylus tenuis* may decrease. Geographically, there may be increasing potential occurrence of *Parelaphostrongylus tenuis* (range expansion) where *Alces alces* and *Ranger tarandus* are likely to decline (range reduced). Where there is minimal spatial overlap (with *Odocoileus virginianus*), *Alces alces* and *Rangifer tarandus* are likely to increase (range expansion). Though there was southward range contraction of *Alces alces* and *Rangifer tarandus*, parasitism may have exacerbated climate-mediated southern range contraction of *Alces alces* and *Rangifer tarandus*. This probably may be due to little or no overlap of the two cervid hosts (*Alces alces* and *Rangifer tarandus*) with *Odocoileus virginianus* (reservoir host). Parasitism had limited influence on northward range expansion of *Alces alces* and *Rangifer tarandus* (Feldman *et al.* 2017). In this example, one host (*Odocoileus virginianus*) mediates the interaction between another host (*Alces alces or Rangifer tarandus*) and a common parasite (*Parelaphostrongylus tenuis*).

Life-history traits and demographic constraints influence colonization potential of partner species of obligate mutualistic and parasitic interactions (Kada *et al.* 2017). This shows that colonization front dynamics have consequences on distribution limits of these partner species (Alzate & Ostein 2022). Change of the distribution limits of partner species has both genetic and phenotypic consequences for partners of such interactions. These consequences may be different for the partner species as a result of the differences in their life-history traits (Couet *et al*. 2022; Vidal *et al*. 2021). This indicates that spatial sorting at the colonization front is expected to affect the partner species differently (Saastamoinen *et al.* 2022). The change of the distribution limits of partner species (expansion or contraction) is influenced by partner species with stronger dispersal abilities who are more likely to be at the colonization front. Where colonization and gene flow depend on host-mediated dispersal, the time the partner (symbiont) spends with the host affects the dispersal potential of the partner (Kada *et al*. 2017). Partner species (symbionts) with phenotypes that promote rapid colonization of the host are likely to prevail (Ganeson *et al*. 2022; Tivey *et al*. 2022) and where the association is not beneficial to the host it may lead to destruction of the interaction (mutualistic interaction) or the interaction becomes transient.

The consequences of range shift and colonization front dynamics have only been studied in the mutualistic interaction between plant (*Leonardoxa africana*) and its obligate ant (*Petalomyrmex phylax*) with another ant (*Cataulacus mckeyi*) being parasitic on the mutualistic interaction (Leotard *et al*. 2009; Mickey 2000; Guame *et al.* 1997; Guame & McKey 1999). This study was done in the rainforest along the coast of Cameroon. In the mutualistic interaction, the plant host *Petalomyrmex phylax* (ant) and the ant protects the plant from phytophagus insects (Figure 5). The species distribution model predicts that the three interacting species have probably undergone recent southward expansion during the Holocene period. This range expansion coincided with the last forest expansion in the area. The two ant species (*Petalomyrmex phylax* and *Cataulacus mckeyi*) showed three phenotypic distribution traits; higher dispersal capacity at the colonization front as compared to other parts of their range, higher ratio of sexual females relative to workers, and larger wing size and body mass of foundresses. These are likely due to spatial sorting (Leotard *et al*. 2009; Mickey 2000; Guame *et al*. 2000). Thus, the ant species invest less in colony growth because only workers are used for defending the plant, and the behavioural investment by workers in defending the plant was lower at the colonization front (Mickey 2000; Guame 1997). At the colonization front, the ants showed signs of less mutualistic phenotype (transient) as exhibited by the reduced investment in growth relative to reproduction and lower investment by workers to defend the plant. However, the plant did not show any sign of less mutualistic or more dispersive phenotype. The plant (*Leonardoxa africana*) has a relatively longer generation time as compared to its mutualistic partner (*Petalomyrmex pyhlax*) and as such the usual ant strategy at colonization front replaces the transient less mutualistic strategy, and evolution of less mutualistic phenotypic plant is not likely due to time constraint. Consequently, the mutualistic association between *Leonardoxa aficana* (plant) and *Petalomyrmex phylax* (ant) is maintained. Though the association is maintained, it provides insight into how a breakdown could occur in partners of obligate mutualistic and parasitic interactions with different life-history traits.

3.3 Sudden climate change on potential extinction of partners of obligate interactions

Climate fluctuations have caused extinction of species in the past, and it is predicted that there will be more extinctions in the future. A key characteristic of current climate change is the presence of extreme climatic events (Gimenez *et al.* 2022). Major mass extinctions of species occur during sudden climate changes due to their exposure to recurrent and extreme climate events usually at short durations (Kaiko 2022; Harris *et al*. 2020; Lohmann *et al*. 2020). The difficulty for species in this situation, is their inability to adapt or shift their ranges because of time constraint. In obligatory mutualistic and parasitic interactions, the partner species respond individually to climate change. Consequently, the following outcomes are predicted: The interaction between the partner species may persist but severely affected or the sudden change may be beyond the tolerance level (range) of one of the partners. For the latter, the less affected partner species can survive on its own until the more affected partner recovers to ensure possible re-formation of the interaction. This may occur depending on the capacity of the affected partner to recolonize empty host niches, life-history traits of the partners, dispersal ability of the affected partner, nature and degree of dependency between partners and the duration of the sudden climatic event.

In the Western Pacific basin, the plant *Ficus pedunculosa* var. *mearnsii* (Mearns fig) forms an obligate mutualistic interaction with pollinating wasp species on the shoreline of Hengchun Peninsula of Taiwan island (Chui *et al*. 2017). The Mearns fig is pollinated by females of single species-specific agaonid wasp and the fig tree provides oviposition sites for the pollinating wasp, and food for its larvae. The wasp uses the syconia (enclosed inflorescence) of the plant to complete its life cycle. The Mearns fig tree exclusively grows on the uplifted coral reef remnants producing syconia throughout the year. Syconia also serve as food for frugivores and in the tropics. A pollinating wasp lives for few days and must find a receptive Mearns fig (with syconia) within hours of its birth. Thus, the receptive syconium is crucial for maintenance of the mutualistic interaction. Since the Mearns fig tree are produced all year round, it allows pollinating wasps to find receptive figs within range and on time. During the typhoon season, the Mearns fig trees lose their leaves and syconia and pollinators (wasps) inside the plant (Bain *et al*. 2014). It is estimated that typhoons affect Mearns fig population annually

(Tu *et al*. 2009). Moreover, the recovery rate of Mearns fig after typhoon is hampered by the frequency of the typhoons. After the typhoon, the few surviving Mearns fig trees depend on pollinating wasps from other populations to pollinate them so as to be able to recolonize locally. This is often a slow process and sometimes may not happen as a result of the complete destruction of the Mearns figs. Due to the recurrent destruction of leaves and syconia and poor recovery of the Mearns figs, both the fig trees and obligatory wasp populations may be at risk of local extinction (Chiu *et al*. 2017; Nicholls & Cazenave 2010).

El Nino-Southern Oscillation (ENSO) is a climatic event that occurs every 2 to 7 years and can last for 9 to 12 months in the Pacific Ocean. This abrupt event leads to increase of sea surface temperature in the eastern Pacific and eventually the whole region (Xiao *et al*. 2022). Records from ENSO show that the wasp (Agaonidae) and fig tree form an obligatory association where the wasp pollinates the plant and also lives on a portion of seeds produced by the tree. The ENSO event of 1997-1998 is reported to be the strongest resulting in extreme drought and loss of fruits and leaves of several fig trees in Borneo (Harrison 2000). The duration of the drought exceeded the life span of the pollinating wasp species and they became extinct locally. Though the fig trees survived the drought, fertilized fig plants and pollinating wasp species were absent six months after the drought (Harrison 2000). The obligatory mutualism between the fig and pollinating wasp was recovered. This primarily was due to the surviving pockets of the pollinating wasp species having short generation time and efficient dispersal abilities to recover the mutualistic interaction. However, the temporarily breakdown of this obligate mutualism as a result of the abrupt climate change (El Nino-Southern Oscillation) is likely to impact on other local species who depend on the Fig/ fig-wasp mutualism or on the fig plant as a keystone species.

In another example in the Pacific region, coral reefs (host) form obligate interaction with dinoflagellates (Symbiodinium). The symbiont also helps with the calcification of the skeleton of the corals. ENSO causes increase in sea surface temperature leading to bleaching of the corals. The cells of the corals (host) are damaged by oxygen radicals produced by the symbiont. This leads to expulsion of the symbiont and eventual breakdown of the coral-dinoflagellate mutualistic interaction, resulting in the death of the corals (Shafiqa-Yusof & Radzi 2022; Parkinson & Baums 2014). The recurrent variability of ENSO causes damage and death of corals (Hoegh-Guldberg *et al*. 2017; Hoey *et al*. 2016). The responses of corals to Holocene climate fluctuations may provide insight into how the marine ecosystem may respond in the future.

4. Observations and conclusion

The responses from obligate mutualistic and parasitic interactions to past climate change would help to improve on the understanding and prediction of how the ecosystem would respond to current and future climate change. However, data on the above is limited as found in this review. Any effort that removes constraints and ensures more data on the effect of past climate change on obligatory interactions is critical. First, there is the need for improvement in the tracing of demographic and evolutionary events that affect organisms. Second, enhancing and improving data collection on obligate mutualistic and parasitic interactions in the tropics to help obtain appropriate and sufficient models to resolve the difficulty of timing biological events. Tracing of both demographic and evolutionary events of organisms, and climatic fluctuations on organisms in the paleontological records with good precision allow for reliable correlation of biological events with climatic events (Mancuso *et al*. 2022; Baltar *et al*. 2019). Presently, climate change can be traced in the paleontological records with relatively good precision but that of demographic and evolutionary events that affected organisms face challenges including not being able to reconstruct recent evolutionary history from fossils (Woolley *et al*. 2022; Mongiardino *et al*. 2021). To improve or eliminate the above constraint, there is the need to enhance the dating processes. For most organisms, the lack of fossils of appropriate age makes calibration very difficult. Dating biological events from DNA sequencing requires use of molecular clock (dos Reis *et al*. 2015). However, there are high variabilities in both speed of evolution and mutation rates (Ho *et al*. 2020; Skeels *et al*. 2022). The use of relaxed molecular clocks has improved the confidence of dating using DNA sequencing. Moreover, dating of demographic events has improved over the period with the use of statistical methods that rely on Bayesian inferences (Otarola-Castillo *et al*. 2022; Bijak & Bryant 2016). Building accurate models of population dynamics and evolution needs improved knowledge on the processes shaping the evolution of species and populations. With recent advancements, the challenges facing molecular dating are gradually being resolved (Guindon 2020). Molecular dating appears to be very promising in the quest for better understanding of biological effects of past climate change. With effective collaboration between experts and model approaches, molecular dating will be crucial in dating past evolutionary events to provide insight into species dispersal, diversification, and demography.

Several researchers have indicated that the tropical ecosystem is relatively stable and appropriate for studies on obligatory mutualistic and parasitic interactions. These interactions have partner species which are specialized and more specific (Weber & Keeler 2013; Salkeld *et al*. 2008). The number of parasites per host (Salkeld *et al*. 2008) and number of plants with extraforal nectar (Weber & Keeler 2013) are relatively higher in the tropics than temperate areas. It has been acknowledged that biotic interactions are more specialized in the tropics, though with some reservations (Moles & Ollerton 2016; Coley & Kursar 2014). Moreover, the ant (specific)-plant (myrmecophic) symbiotic interactions which are diverse with different levels of specificity, make these interactions suitable models for comparative analysis. The interacting species being highly specific and specialized make them sensitive to environmental conditions. Again, this ant-plant symbiotic interaction appears and breakdown during the course of evolution. These attributes enhance the capacities of these interactions to detect past climate fluctuations. The ant-plant symbiotic interactions are generally found in the tropics and spread into the temperate zones, making the case for relatively more model systems in the tropics for studying the effect of past climate fluctuations on obligate mutualistic and parasitic interactions. The partner species of these interactions often share the same biogeographic history and are interdependent, making them suitable for investigating the effects of climate change on ecosystems.

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Conflict of interest

The author declares that there is no conflict of interest regarding the publication of this paper.

Data Availability

The data used to support the findings of the study are available within the article.

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FIQURES

Figure 1: Aphids living with their endosymbiont *Buchnera aphidicola* (Hansen & Moran, 2011)

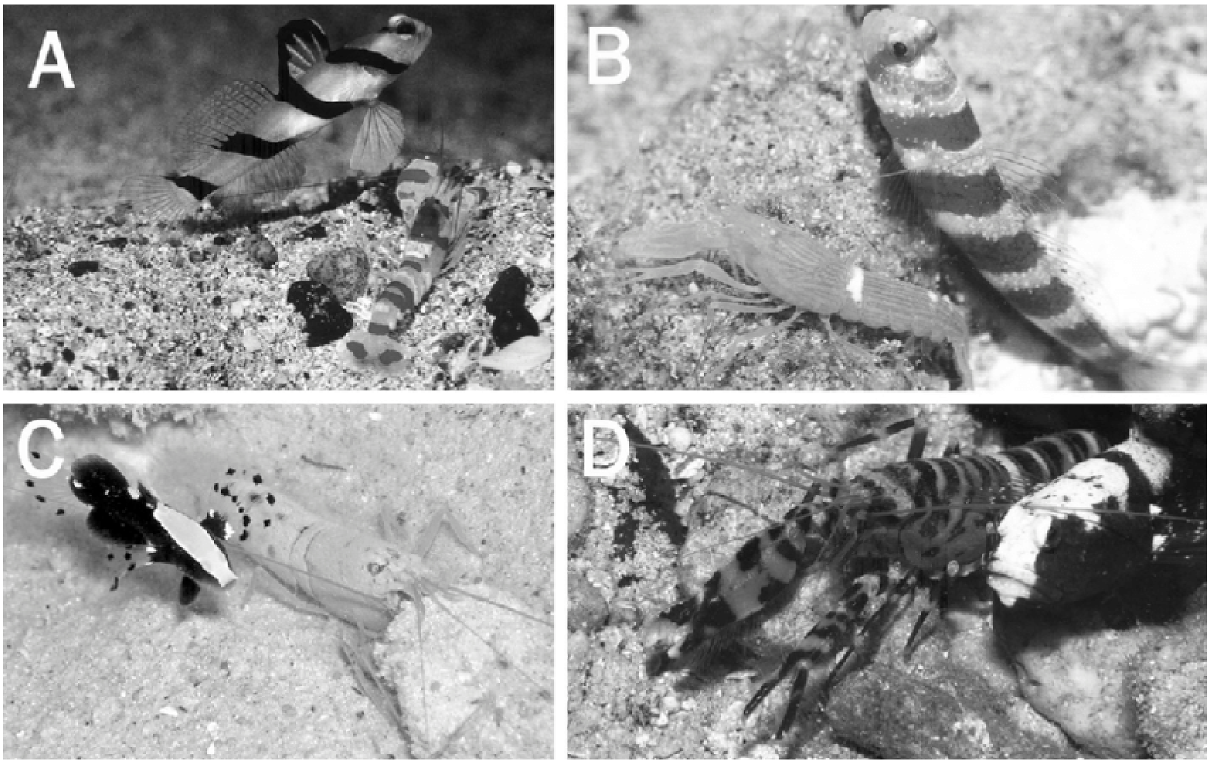

Figure 2: Associations between gobies and alpheid shrimps (Karplus, 1987)

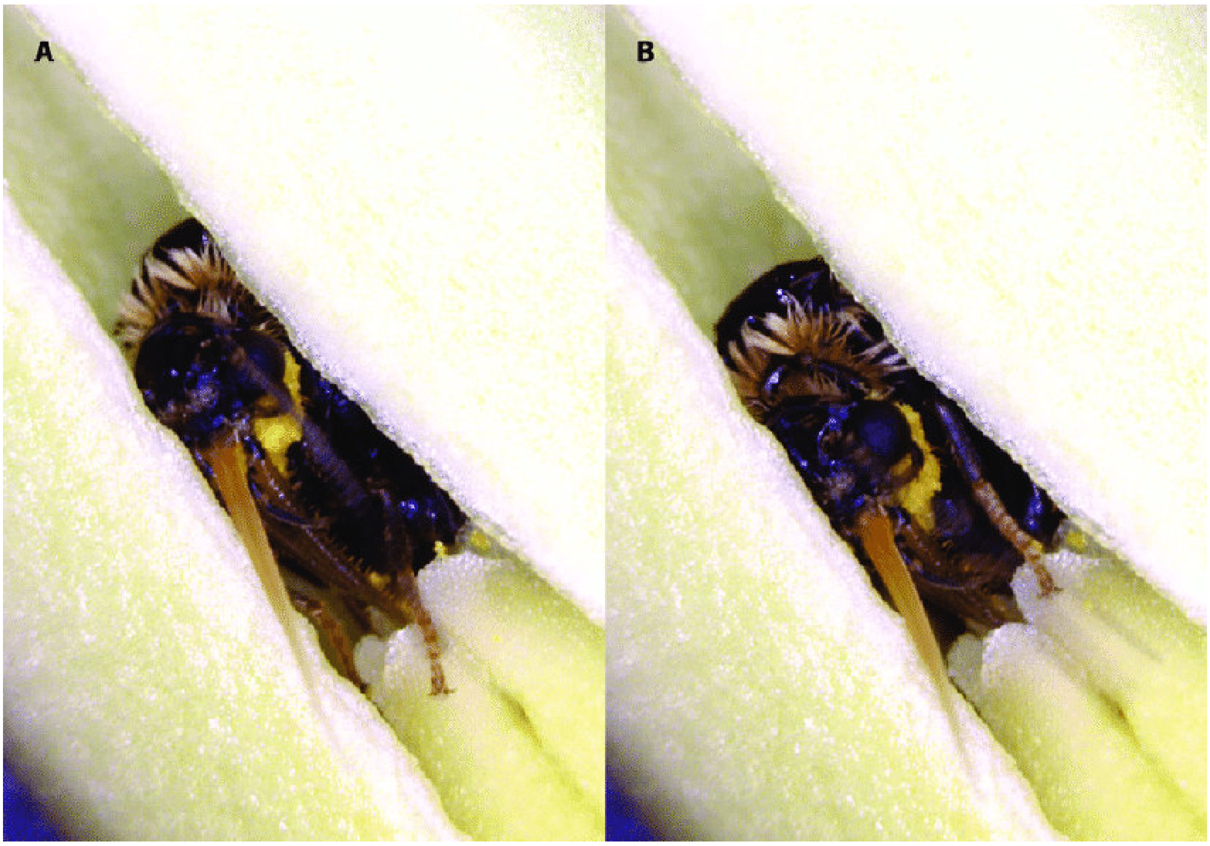

Figure 3: Female *Tegeticula antithetica* pollinating Yucca tree (Cole et al., 2017)

Figure 4: *Ephicephala* sp. (moth) ovipositing into female *Breynia oblongifolia* flowers (Finch et al., 2019)

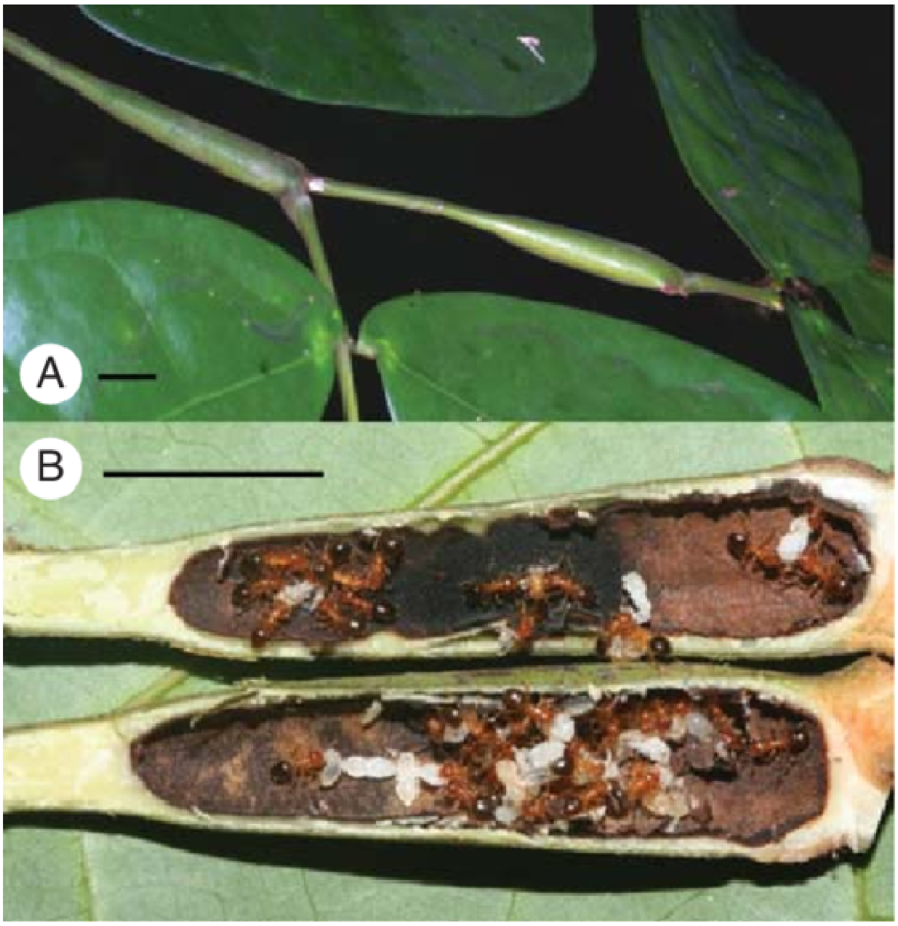

Figure 5: Characteristic feature of the symbiosis between *Leonardoxa africana* Subsp. *africana* and ant *Petalomyrmex phylax.* (Mckey, 2000)