TREE-HOLE AQUATIC HABITATS: INHABITANTS, PROCESSES AND EXPERIMENTS. A REVIEW

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Abstract

Studying small confined habitat has two fold advantages for ecological research. Firstly, its importance as habitat to a micro-ecosystem, and secondly its applications in experimental research. Tree-hole aquatic habitat is such a habitat having a considerable importance as micro - habitat for numerous significant species, especially for disease spreading invertebrates, which act as model systems as they have tractability and generality at laboratory scale studies. This review highlights profiles of tree-hole aquatic habitats and ecological relationships of its inhabitants supported by experimental evidences in peninsular India.

Keywords: Aquatic insects; Phytotelmata; Tree hole; Trichoptera

Introduction

Tree-hole aquatic habitats grouped under the broad class of phytotelmata-plant held water are in the main stream ecological research starting from seminal studies by Ludwig Varga and Albrecht Thienemann [1]. The initial curiosity of what will be there in these "hanging aquaria", led to major explorations in various types of phytotelmata, such as pitcher plant flower bracts, bamboo inter-nodes, and bromeliads in different parts of the world [2]. Epidemiological importance of these habitats as breeding place for several disease vectors and its wide distribution especially in the case of tree-hole aquatic habitat transformed the initial curiosity into a hot epidemic research topic [3-5]. The autecological epidemic research on treehole aquatic habitat then led to community level studies [1, 6] looking into the ecology, community determinations and realization as important tools for studying these processes.

Water-filled tree holes (Fig. 1) are observed all over the world as one of the important characteristics of tropical forests [2, 7]. Tree holes are formed by intrinsic growth pattern of tree

or extrinsic agencies such as wind breakage, forest fires, hole excavation by organisms such as wood peckers, insects, or microbial injuries [1, 8]. Tree-hole aquatic habitats are classified into pan tree holes and rot tree holes based on the growth pattern having inner lining of bark not having the bark lining mostly formed by external forces [1]. Based on morphology of tree-hole opening they are again classified as pan tree holes which have higher opening area than depth, and bowl tree holes, which have higher depth than opening, area and slit holes having narrow opening [9]. A wide array of organisms yet simplistic fauna largely shared by insects, inhabit it [10, 11]. The habitat is functionalized by allochthonous energy sources, derived from litter decomposition and nutrient leaching through stem flow. The confined, spatially distributed and wide availability of them instigate discreteness, patchiness and replications in forested land [2, 12]. These features, along with simplicity of community, allow them to duplicate with artificial analogies of controlled characteristics. This makes them an important natural microcosm for carrying out ecosystem experiments having wide generalization [13]. In the last four decades, extensive research was carried out in various vital processes of making it to understand this unique habitat [1, 2, 6, 11]. The present review highlights the predominant communities of tree-hole aquatic habitat, its functionality and ecological experiments.
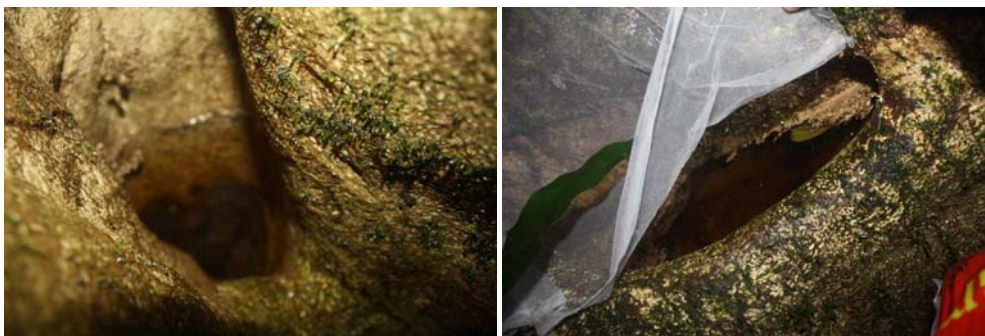

Fig. 1. Tree-hole aquatic habitats

Methodology

Three search engines were used to collect review of literature on the research on the Tree-hole Aquatic habitat. The Web of Science from Science Citation Index (Thomson Reuters, New York, USA) was searched from 1950 to the present (on 18 August 2013), Biological Abstracts (Thomson Reuters, New York, USA) from 1970 to 2012 (18 August 2013) and Google Scholar in 'Biology, Life Sciences and Environmental Sciences' subject area, with keywords 'aquatic insects', 'phytotelmata' and 'treehole' up to 18 August 2013. Despite Google Scholar yielded a large number of results, this still may not be comprehensive due to several limitations, including biases in the journals crawled by Google Scholar. To this, it is also added information collated from reports, books and papers that came across over the last decade of research on this habitat. Snowball approach was used to find additional published and grey literature. Despite these efforts, this review is, at most, only an overview of the different fields of research since several publications in very specific journals or institutional reports may have gone unobserved.

Communities

Tree-hole aquatic habitat harbors litter-detritus based communities of bacteria, fungi, algae, protozoa, platyhelminths, rotifers, gastrotrichs, nematodes, oligochaetes, crustaceans, insects and amphibians [6]. Communities in tree-hole aquatic habitat are classified into three

groups based on their degree of utilization of the habitat as accidental, facultative and specialist [1, 14].

Microbes

In fact tree-hole aquatic habitats are heterotrophic microbial ecosystem. Very little is known about their community composition in it. Most of the studies consider the microbes and detritus as single ecological unit and concentrate more on insect populations [11, 15]. Recent study on bacterial community structure in tree-hole aquatic habitat of culicid *Ochlerotatus triseriatus* in Michigan, USA recorded 29 families from 5 phyla of Bacteroidetes, Proteobacteria, Actinobacteria, Verrucomicrobia and Firmicutes. The study also indicated Flavobacteriaceae of Bacteroidetes phyla as an important food of mosquito larvae [16]. Around 45 fungal species included in aquatic, aero-aquatic and dematiaceous hyphomycetes are recorded from tree-hole aquatic habitats of Hungary [17]. The study also raised an important question about the occurrence of water dispersed spores in tree-hole aquatic habitat. Around 40 species of protozoans have been recorded from European beach tree holes [18]. Similar study in California, USA, found that protozoan community is dominated by six families of Ciliophora namely Parameciidae, Erionellidae, Discocephalidae, Tetrahymenidae, Chilodonellidae, Colpodidae species [15].

J.B. Lackey in 1940 [19] observed the occurrence of specialist colorless flagellates, diatoms and absence of photosynthetic algae form the tree holes of Eastern USA. He concluded that the extreme habitat in terms of nutrient concentration is excluding photosynthetic forms from tree-hole aquatic habitat. M. Devetter in 2004 [20] studied tree-hole communities in Czech Republic and reported that most abundant groups in tree-hole aquatic habitat are Nematodes, Rotifers, and Diptera. He found six different species of Rotifers in tree holes from the study area.

Macroinvertebrates

Insects are the most studied group in tree-hole aquatic habitat (Table 1). Five orders of aquatic insects namely Diptera, Coleoptera, Heteroptera, Odonata and Trichoptera have been recorded from tree-hole aquatic habitat. The comparison of insect order availability in tree-hole aquatic habitat of different geographic locations indicates the obvious species richness in tropical countries (Fig. 2).

Table 1. Aquatic insects in tree-hole habitat.

S.N	Order	Family	*Genus*	Reference
1	Diptera	Anthomyiidae		10
		Calliphoridae		10
		Cecidiomyiidae		10,20
		Ceratopogonidae		1,10,14,20,21,52,54,59,91,93,94,
		Chaoboridae		10,14
		Chironomidae		1,10,14,20,21,52,54,59,91,93,94,
		Culicidae	*Aedes*	1,4,5,12,14,20,,52,54,59,90,94
			Anopheles	1,14,59
			Armigeres	12,52
			Culex	4,5,12,14,52,54,90
			Haemagogus	14
			Limatus	14
			Orthopodomyia	14,12,52,54
			Toxorhynchites	4,14,21,52,54,91
			Trichoprosopon	14
			Tripteroides	12,52,54,91
			Uranotaenia	12,52,55,91
		Muscidae	*Muscomorpha sp.*	10,20,52
		Mycetophylidae		20
		Phoridae		12,52,55,91

		Psychodidae		10,14,93
		Sciaridae		20,52
		Stratiomyidae		10,14,52,54,59
		Syrphidae		1,10,20,21,52,54,91
		Tabanidae		10
		Tipulidae		10,14,21,52,54,91,94
2	Coleoptera	Dytiscidae		21,91
			Copelatus	14
			Laccophilus	14
		Hydraenidae		20
		Hydrophilidae	*Ctogdia*	10
		Psychodidae		93
		Ptilodactylidae	*Prionocyphon serricornis*	14
		Scirtidae (Helodidae)		1,4,10,14,21,52,54,59,91,
3	Hemiptera			14
		Notonectidae		21
		Veliidae		10
4	Odonata			91
		Aeshnidae		10
			Gynacantha membranalis	14
			Triacanthagyna dentata	14
		Coenagrionidae		10
		Libellulidae		10,21,54
			Libellula	14
		Megapodagrionidae		10
			Percinemis triangularis	91
			Lyriothemis cleis	91
			Indaeshua grubaueri	91
		Pseudostigmatidae	*Mecistogaster linearis*	14
			Mecistogaster ornata	14
			Megaloprepus coerulatus	14
5	Trichoptera	Limnophilidae		10
		Conoesucidae	*Pycnocentria*	94
		Leptoceridae		21
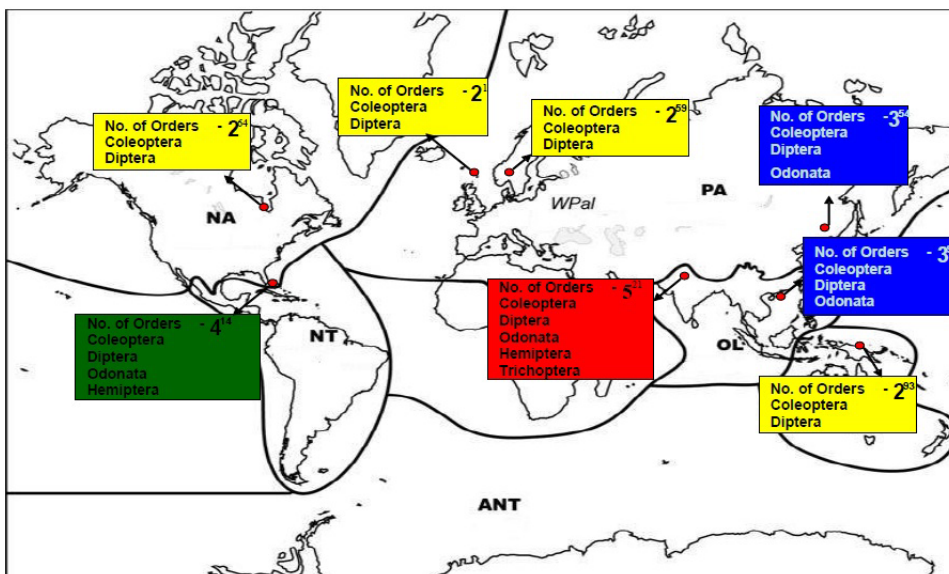
Fig. 2. Comparison of aquatic insect orders in tree-hole habitat in the World.

Other than insects Nematodes, Crustaceans, Annelida and Arachnida classified as accidental inhabitants, have also been recorded in tree-hole aquatic habitat [14, 21].

Vertebrates

Yanoviak [14] reported three frog species such as *Agalychnis callidryas*, *Dendrobates auratus* and *Physalaemus pustulosus* breeding in tree-hole aquatic habitat. He also reported occasional visiting of *Eleutherodactylus* spp. frogs and *Sphaerodactylus lineolatus* gecko in tree-hole aquatic habitat of Panama. The recent survey on tree-hole aquatic habitat in tropical forest of India reported breeding of tree frog *Ramnella montana* and sighting of gecko *Cnemaspis sp.*, Malabar Pit Viper *Trimeresurus malabaricus* [21].

Processes

Processes functionalizing tree-hole aquatic habitat can be divided based on the participating components namely energy source, habitat characteristics, and vital determinants such as colonization, community interactions and environmental heterogeneity of surrounding ecosystem (Fig. 3). Tree-hole aquatic habitats are integrated with surrounding ecosystem in terms of necessary allochthonous energy sources and for dispersal and colonization of life forms in it [1]. The colonized communities in it depend on habitat characteristics, interaction within them and environmental heterogeneity.

Colonization

Colonization poses answer for the intriguing question of why the particular organism is in tree-hole aquatic habitat as every other habitat [11].
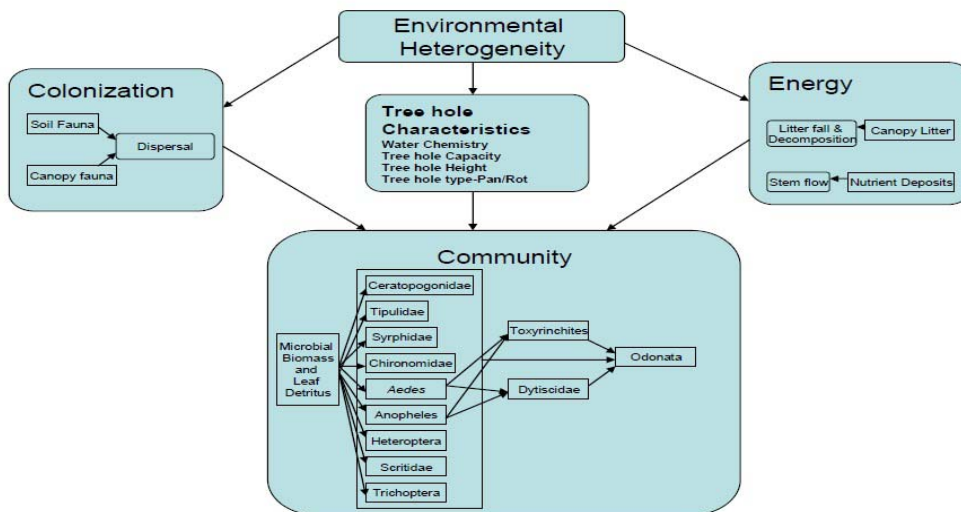
Fig. 3. The essential processes, interrelationships in community organization
of tree-hole aquatic habitat in a tropical rain forest

Colonization involves series of interlinked events such as dispersal, arrival and establishment in the particular habitat [6]. Dispersal can be either active means of aerial flight or passive means of completely relaying on other external agents such as vector or wind [22]. Other than colonization dispersal is detrimental for gene flow and evolutionary divergence in spatially discrete fresh water habitats such as tree-hole aquatic habitat [22]. Passive dispersal studies using container habitats reveal that it is carried out largely by air current, rain water, soil

splashing and flying vectors. The species arrival in a container habitat is inversely related to height and distance from local species pool. The study also indicated the stabilization of organism arrival and establishment with time, due to inter-specific interactions and community level prevention of successive invasion [23]. A similar study with aquatic insects of the habitat indicated their important role in passive dispersal of microorganisms such as algae, euglenoids and protozoan during their interaction with aquatic habitat for perching, foraging and oviposition [24]. Studies on relative migration rate of host and parasite improve the knowledge on passive dispersal by winged flies on phylogenetically lower microbes [25]. It was observed that hosts migrates and colonize more than parasites and directly influence the local adaptation of parasites in the tree-hole aquatic habitat. An extensive review of colonization in phytotelmata by B.J. Maguire [6] gives important direction in the topic. He speculated the divergence in colonization curves in temperate zones, and tropical zones based on efficiency of dispersal. Colonization, extinction curves in phytotelmata is largely influenced by community level interactions and habitat heterogeneity. A series of studies using pitcher plant phytotelmata as model system give greater insight into the invasion success, and dispersal rate on species composition [26, 27]. It is highlighted that differential influence of migration, predation and resource availability on invasion success, for a similar community. Based on higher dispersal frequencies, regional species richness increased and local variances were reduced. The active dispersal studies on oviposition behavior of mosquitoes in tree-hole aquatic habitat show that along with active dispersal, passive dispersal and spatial heterogeneity have non negligible influence on tree-hole mosquito larvae colonization [28]. An advance study on cues influence on mosquito oviposition indicates that litter bacterial derived chemical cues are influencing active dispersal in container habitats [29]. Studies in *Heliconia* bracts phytotelmata indicate their colonization by insects function as ecological islands and their species richness is positively influenced by habitat number and negatively influenced by habitat size [30]. Later, these speculations were further narrowed between phylogenetically lower and higher organisms. Lower organisms such as microbes, phytotelmata are acting as island due to their non specialization and inevitable extinction while habitat is dried out. But higher organisms such as flying insect's phytotelmata are acting as swamps due to their selective colonization and specialization in utilizing the available resources in habitat [31]. Along with these colonization processes, the organisms which are adaptable to the rapidly varying habitat and biotic characteristics, are successful colonizers in tree-hole aquatic habitats.

Energy source

Tree-hole aquatic habitat community is functionalized by pulsed form of allochthonous energy input derived from plant, animal detritus and inorganic nutrient transport from stem flow and through fall [1, 18, 32-40]. Various factors especially detritus processing, quantity and quality of detritus input, hydrology of the tree-hole and rain pattern of the area are directly influencing the formation of heterotrophic detritus based system in tree-hole aquatic habitat [18, 41]. As a basic heterotrophic system, energy is derived from conversion of complex organic compounds into simpler forms by decomposition. The decomposition of leaf litter was carried out through two functional groups namely Particulate organic matter (POM) generation and Dissolved organic matter generation (DOM) from coarse particulate organic matter (CPOM) that is intact fallen leaf litter [42, 43]. Soluble organic as well as inorganic matter is leached out into DOM pool shortly after the litter is immersed in the water. The leached out remaining CPOM undergoes transformation into fine particulate matter (FPOM) in the habitat. The transformation is carried out by interaction of microbial conditioning, metabolism and mechanical shredding by macro invertebrates. Microbial decomposition is largely carried out by fungi and bacteria in tree-hole aquatic habitat [18, 44]. Aquatic hypomycetes of fungi primarily colonizes and dominates the leaf litter which then gives way to bacterial populations [34, 44]. Aquatic hypomycetes produces enzymes like pectinases, hemicellulases and cellulases for

breakdown of plant litters [44]. Nitrifying, denitrifying and sulfate reducing bacteria are constituent of litter decomposing bacterial populations in tree-hole aquatic habitat [18]. Detritus input, largely of plant origin has very limited quantity of essential inorganic nutrient for the microbial decomposers. This limitation is surpassed by relying on dissolved inorganic nutrients derived from stem flow and animal detritus [18]. Mechanical shredding by invertebrates call it as shredders has considerable influence on litter decomposition in tree-hole [34, 44]. Since these invertebrates such as coleoptera and tipulidae are abundant in tree-hole aquatic habitat, transforms CPOM leaf litter into FPOM and make available the unconsumed shredded litter to decomposing microbes and higher grazing insects [44, 45]. D. Fish and S.R. Carpenterin 1982 [34] reports about physical abrasion caused by mosquito larvae in tree-hole acts as shredders and speculate it as the typical behavior of tree-hole colonizers. Experimental studies on the presence of invertebrate carcasses in tree-hole model containers shows the importance of these resources as faster decaying, supporting with limiting nutrients and as reliving the resource competition between communities of tree-hole aquatic habitat A similar study using Scritidae feces shows that availability of this resource as animal detritus increases the overall well being of the mosquito larval population in the tree-hole model system [46]. Stem flow and litter flow are considered as the important means of nutrient cycling in canopy and floor in forest ecosystem [47, 48]. Studies with influence of stem flow on tree-hole aquatic habitat shows that it facilitates essential nutrients especially nitrate, sulfate, inorganic cation and as well as flush the toxic metabolites of ammonium, hydrogen sulfide out of habitat [18]. The impact of stem flow on tree-hole aquatic habitat is considered as "intermediate level disturbance" [49], "Type I perturbation" [50], latter it was reviewed as "Positive or necessary" [18] disturbance to tree-hole aquatic habitat. Structural and formation characteristics likely influence the stem flow in a tree hole. Tree-hole such as pan holes having inner lining of tree bark are having connection with stem and thus facilitated with high stem flow than rot tree holes which are not having inner bark lining and thus lacks a connection with stem. Hence the stem flow is negligible or absent in this type tree holes [18].

Habitat characteristics

Habitat characteristics of tree-hole can be divided as structural characteristics and Constituent characteristics. Structural characteristics indicate the size, type and locality of habitat. Constituent characteristics involve water medium, chemical nature of the medium and resource availability. Former character determines durational stability and the latter one determines resource level and constancy of the communities in the habitat and it depends completely on the former one [51]. Tree-hole is formed by multiple interacting factors of growth characteristics of tree to form pan holes and uncertain external agency to break the tree branches to form rot holes. This leads to the availability of structurally variable tree holes in an area [1, 52]. The size of the tree-hole largely influences its further characteristics of persistence of habitat and community constancy in it [12, 52-56]. Study conducted for experimentally determining the influence of habitat stability on tree-hole mosquitoes shows that the probability of water and community availability in a container is positively correlated with rainfall intensity of the area and size of the container [12]. The habitat size influences food web structure by mechanisms of persisting unstable food webs in larger habitats [55]. The interacting factors of higher size and subsequent larger resource base in tree-hole aquatic habitat show higher species richness and biomass. The size distribution of habitat influences the diurnal abiotic characteristics and variability among local and regional species richness [52, 54, 57]. Location of tree-hole like the height from the ground negatively influences species richness of tree-hole aquatic habitat [53]. It is hypothesized that disturbance regime on high canopy tree-hole rightly influence the low species richness in it [53]. Water is collected in tree-hole through fall and stem flow, removed from it by evaporation or seepage into underlying wood [1, 17, 58]. Thus the rain and solar intensity of the area directly influence the water availability in tree-holes. The

water stagnation is always not a permanent property in tree hole. During heavy rain tree-hole acts as a "pool in temporary vertical streams" [18] and or as a "natural open flow chamber" [17]. This property has greater implications on tree-hole water characteristics and to a larger extent on the community in it [17, 18]. The phenomenon results in considerable dilution of nutrients and toxins of inhabitant metabolisms in tree hole. This changing hydrological condition is speculated as favorable for availability of certain species in tree-hole habitat, evidently for fungal species. Studies on water characteristics of tree-hole show that in terms of high nutrient concentration and acidity, they act as "extreme habitat" for the communities in it [18, 32, 59, 60]. It is observed that the nutrient concentration and characteristics of treehole water have considerable effect on communities. S.R. Carpenter [32] demonstrated that water chemistry of tree-hole had an effect on the life history of mosquitoes. E.D. Walker in 1991 [18] explained that stem flow has considerable implication on nutrient dynamics, bacterial populations and mosquito productivity. C.J. Paradise in 2009 [59] shows that abiotic factors, mainly water characteristics determine the biotic interaction and acid deposition has complex impact on tree-hole communities. J. Schimdl in 2008 [60] showed that the food web in tree-hole is mainly influenced by bottom up factors of environmental/habitat characteristics, especially water chemistry with no part played by top down more complex community level influences.

Community interactions

Community interactions in tree-hole aquatic habitat can be divided as facilitation, interspecific, intra specific competition and predation [11]. Heterotrophic system in tree-hole aquatic habitat is basically unidirectional conditioning of detritus resources in which the higher trophic components depend on conditioning or facilitation of lower trophic organisms. Thus the process of facilitation and processing chain interactions are common community interactions in it [61]. Several of studies in tree-hole aquatic habitat show the processing chain interaction in it. R.L. Kitching and S.L. Pimm in 1985 [62] observed processing chain interaction in tree-hole food webs between coarse detritus browsers Scritidae beetle, Tipulidae and other dipterans as means of transforming coarse into fine detritus. This interaction is also observed by W.E. Bradshaw and C.M. Holzapfel in 1992 [63] in which interactions are observed as transformation of coarse buried detritus into fine suspended detritus by coleopterans and facilitated to mites. Later detailed experiments on tree-hole communities C.J. Paradise and W.A. Dunson (1997) [64] illustrate that processing chain interaction was evident between helodid beetles as detritus shredders, and Ceratopogined midges of deposit feeders. The function of helodid beetles in this system is speculated as 'key stone decomposers' while it determines resource availability and community structure. This speculation was latter confronted as shredders are conditional mediators of resource on mosquito populations, since resource alone is the largest determination of population [65].

Competition or avoidance of competition is considered as the important factor structuring communities [11, 66]. Interspecific and intra specific competition in tree-hole communities are well documented [34, 57, 67-69]. T.P. Livdhal (1982) [67] states that varying concentration of resource and varying density of mosquito cohorts with similar and independent competitive effect on overall composite performance of tree-hole mosquitoes. Similarly D. Fish and S.R. Carpenter (1982) [34] explain that intraspecific competition among tree-hole mosquitoes in relation to resource levels. They showed that larger density of mosquitoes reduces the overall performance of population in terms of larval survivorship, pupation rates, pupae biomass, and total yield. This type intraspecific competition was also observed in tree-hole frogs *Chirixalus eiffingeri* in which the larger tadpoles significantly impacted the growth, survivorship, survival to metamorphosis, the length of larval period, and mass at metamorphosis of younger tadpoles [68]. O.M. Fincke (1999) [57] explains the interspecific competition between two species of Odonata, namely *Megaloprepus Mecistogaster* species, largely influenced by limitation of tree-hole as breeding site and size of the species having competitive advantage over another one. B.

Kesvaraju et al. (2007) [69] show that interspecific and intraspecific competition between native *Ochlerotatus triseriatus* and non native *Aedes albopictus* was influenced by advantage of using high quality food resources by native species and subsequent competitive advantage over another one.

Predation is the major determining community interaction in tree-hole aquatic habitat [11]. It acts in the way by presence of specialized predators in the communities such as larvae of *Toxorhynchites,* odonata, dytiscid beetles or by density dependent facultative predation. Both these predation have considerable influence on structuring tree-hole community or even above explained interactions [11]. By considering direct impact of *Toxorhynchites* on their prey, R.L. Kitching (2001) [11] proposes them as key stone species in tree-hole aquatic habitat. Also O.M. Fincke et al. (1997) [70] illustrate the occurrence of three groups of predators, four species of odonata larvae, one mosquito larvae and one tadpole species from tree-hole aquatic habitat of Panama. These authors also point out the size selective resource mediated predation by odonata in tree-hole habitat. Predation was high in low resource condition and low in high resource condition where the predation effects were minimized by high abundance of mosquitoes and selective predation on large mosquitoes. Studies carried out to assess the predation pressure [71] on bacteria communities shows that bacteria respond to predation by outgrowing the predation pressure or by developing inedible, inactive filaments to their flagellated predators. They also hypothesized the adoption towards predation within 24 hours as the action of chemical stimuli produced by bacteria to predation. A study [72] to assess interaction of community determining factors of disturbance, predation and resource level shows that community composition is altered by those interactions and responded by certain group of communities. M.W. Griswold and L.P. Lounibous in 2005 and 2006 [73, 74] demonstrate that the interaction of predation and resource level determines the survival and coexistence of two species of mosquitoes. Interestingly they found that increased predation is more important for the coexistence of mosquito species *Aedes albopictus* and *Ochlerotatus triseriatus* in tree-hole aquatic habitat. They also found that additive effects in multiple predator interactions.

Environmental heterogeneity

Environmental variability of the habitat influences all those above explained processes. It can be top down processes determining the community and food webs in tree-hole aquatic habitat as explained by R.L. Kitching [11]. As a means to define environmental heterogeneity influence on *Weyomia,* he models the thermal hydro variation in microhabitat of pitcher plant. He observed validation to the model with significant difference in maintenance of fitness variation in *Weyomia* population based on microclimatic effects. This phenomenon was again seen in the case of habitat segregation by tree-hole mosquitoes based on their height and resultant microhabitat preference for oviposition [76]. Tree-hole habitat distributed in different microclimatic condition in Kenyan coast was studied and it illustrated clear segregation in mosquito species based on microclimatic preference of the species. The highest species richness was observed in ecotonal regions with significant reduction in specific dominance. It was further made evident by D.A. Yee and S.H. Yee in 2007 [77] which shows that mosquito population in container habitat was largely determined by surrounding habitat matrix and characteristics. R.L. Kitching in 1987 [78] studied the food web variation in spatial and temporal scales. He observed that Food web similarity is reduced as inter site distance between two tree-hole habitat increases. It showed the spatial heterogeneity determination on food web in tree-hole aquatic habitat. He points out that both "grand" deterministic theories such as competition, resource partitioning or other ecological processes and "local" uncertainties such as environmental heterogeneity have important roles in structuring food web variation in local level. The recent study by C.J. Paradise et al. in 2008 [79] gives further evidence to the role of environmental heterogeneity in shaping the tree-hole communities. Three years of monthly tree-hole census by them show that community composition in it was best explained by local

conditions, spatiotemporal variation and colonization events. The environmental heterogeneity was acting within small spatial distance between habitats as community asynchrony [80]. They conclude that local environmental variability was more detrimental in community composition in tree-hole aquatic habitat than regional factors. D.S. Srivastava in 2005 [81] explains that local processes in tree-hole aquatic habitat may not be scale to global patterns. By comparing the local species richness variation in tree-hole habitat with eight biogeography regions, she elucidated that small scale difference in drought disturbance as a measure of determinant of species richness in habitat explains the pattern in local level but it cannot be a determinant in global scale. This explains that local level community interactions or determinant was obscured to interpolate with large landscape or global level due to the effect of environmental heterogeneity.

Experiments

Experiments are one of the important approaches for ecological research. It gives greater insight about the impact of natural or anthropogenic perturbations on ecosystem processes and its response towards the impact [82]. The experimentation requires tractability, generality and realisms to test the theory and hypothesis of ecological process. Model systems provide these features and are widely used in ecosystem experiments. Natural microcosms are important model systems because of their position between two extremes of experimental models of laboratory microcosms and whole ecosystem experiments. Laboratory microcosm has lacunae of generality and whole ecosystem experiments have lacunae of tractability [13]. These limitations to a certain extend reduced by characteristics of natural microcosms as they are discrete, having naturally colonized simplified community, spatially distributed and long evolutionary history as in the case of tree-hole aquatic habitat, one of the important natural microcosm. The simple self contained communities in tree holes gives an easy manipulation of habitat to control structural, energy regime and community characteristics for ecological experiments. Biodiversity-Ecosystem functionality, dynamic constraints, Impacts of disturbance, Influence of productivity on natural communities is some of the problems addressed by experiments in tree holes.

Relationship of biodiversity to ecosystem functionality and productivity is explained by two principle mechanisms namely 'complementarity mechanism' and 'selection mechanism' [83]. Species rich systems utilize more resources and are more productive because each species uses slightly different resources and overall species richness contributes to productivity, this form basis for 'complementarity mechanism'. 'Selection mechanism' explains that there will be variability between each species to utilize resource and certain species is more productive than others, thus the productivity is average of each species contribution to productivity. There was a speculation that both these mechanisms are interplaying to improve ecosystem functionality [84]. T. Bell et al. in 2005 [85] performed experimental study to assess the influence of tree-hole aquatic habitat bacterial diversity in ecosystem functioning. They found that there is a consistent decelerating relationship between ecosystem services counted as respiration in experiment and increase in species richness. They show that synergistic effect of both bacterial species richness and community composition is more important in ecosystem functionality than selection mechanism in the experimental bacterial community.

The process that structure food web in a community is explained by two principle hypothesis of availability of energy and influence of dynamic constrains [86]. Dynamic constraints are considered as the most important explanation for food web structuring [87]. Dynamic constraints explain that the food web in a habitat may be the resultant of average environmental predictability of the area compared with other localities. B. Jenkins et al. in 1992 [88] demonstrated the influence of dynamic constraints on food web structuring by using

artificial analogies of tree-hole aquatic habitat. In experimental container habitat, the temporal food web dynamics was significantly lowered during natural perturbation of reduced rainfall and the lowering was most pronounced in most productive habitat as similar to low productive habitat. This gives experimental evidence of dynamic constraints/ environmental predictability which determines the local food web structure than availability of energy.

The knowledge of impact of anthropogenic perturbations on ecosystem is imperative to devise management options and conservation. Natural microcosm such as tree-hole aquatic habitat has many advantages to use for experiments devising to assess the impact [89]. Those experiments can explain the direct or indirect effect of impact on multi trophic level with apparent biotic and abiotic dynamics in natural ecosystem. Experiments carried out to assess the acidic deposition effect on tree-hole communities, C.J. Paradise and W.A. Dunson [45], C.J. Paradise and K.L. Kuhn [59] and C.J. Paradise in 1999 [64] shows that the biota of tree-hole habitat is differentially affected by acidic deposition in terms of changes in ionic balance of the water. They also showed that low pH impacted the growth of certain key inhabitants in tree-hole with relation to resource base. It has complex impacts on community interactions by effecting the processing chain commensalisms [90] happens in tree-hole aquatic habitat. They proposed that the tree-hole habitat can be used as a bioindicator of forest ecosystem towards acidic deposition.

One of the widely accepted explanations for increase in species richness with productivity is "more individual hypothesis". It explains that more productivity results in higher abundance and species richness increases as a function of abundance. This hypothesis was tested using tree-hole communities by D.D. Srivastava and J.H. Lawton in 1998 [91] and found that it is insufficient to explain these processes. The experiment shows that though the tree-hole habitat harbors more species according to productivity and not in abundance. They conclude that the process of species richness according to productivity is complex and the explanation prevailing has failed to consider the colonization, extinction pattern and size variability of inhabitants in the habitat.

Conclusion

Though tree-hole aquatic habitats are small and confined, their inhabitants and processes functionalizing in it are much complex and dynamic. This postulates them as a miniaturization of large aquatic habitats with their own specialized characteristics and communities. They are acting as important stagnant aquatic habitat in forest. Their role in large tropical forest ecosystem is yet to be explored with evolutionary linkage on container inhabitant mosquitoes. There is only scanty knowledge about this habitat in Tropical Asian scenario. Their role as essential habitat and harboring a wide variety of organisms, epidemiological importance and application as use full tool for ecosystem experiments make it worthy to investigate this "hanging aquaria" of our tropical rainforests.

Acknowledgements

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