Nest Availability and Origin in Wood for Aculeata Wasps and Bees with Special Reference to Ladakh Region

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Abstract

The Aculeate wasps and some of bee species select woody habitat for nesting and form guilds in preexisting wood cavities. The guild form of existence in woods is an important component of various ecosystem services like predation, diversity equilibrium and pollination. The variation in species diversity parameters is clearly associated with environmental structure, habitat, substratum, foraging resources, and interaction with other organisms. Generally, in bees and wasps the nesting periods is most crucial and it demands the abundant resources in the form of habitat, forage (food) and plant diversity. Females in both wasps and bees construction their nesting cavity during maximum of their life cycle, followed by provisioning of young ones. We observed maximum dominance of two wood nesters (*Xylocopa valga* and *Megachilidae* species). Under cold arid conditions of Ladakh maximum percentage of cavities and holes for bee and wasp nesting are present in older willow, followed by populous, apricot and apple. Due to low microbial activity the availability of nesting cavities in hard wood are deficient, contributing to lower pollinator diversity in Ladakh region. Unlike soil nesting species, the real causes of wood nesting by wasps and bees is unknown. The aim of the current paper is to highlight the proximate reasons of nest choosing state, setting effective conservation and management procedures for Hymenopteran species.

Keywords: Wasps, bees, woody habitat and species diversity.

Introduction

For agricultural purposes the bees compete with other species for food and nesting (LeCroy *et al.,* 2020). The ecological systems and physical structures of environment certainly affect the reproductive success of solitary wasps and bees. Research suggests that nesting period is a critical phase in life cycle of all wasps and bees. The solitary wasps and bees grow through maximum proportion of the life cycle for constructing and provisioning their nests. Nesting behaviour and all other its related activities are affected by nesting sites, food availability, anthropogenic factors, and landscapes categories. Construction of nesting cavity, provisions, egg-laying are the major activities in which females invest much of their life time (Antoine and Forrest, 2020). The well undisturbed nesting sites and good foraging areas increase the chances of offspring survival till their adulthood (Tlak *et al*, 2014; 2015). Even though the females exhibit adaptive behaviours, the individuals which choose preexisting cavities as nesting sites were found less fertile then females of soil dwelling species. Nesting features of species (Aculeate species) which prefer preexisting cavities have different nest construction features but all have cells as a common characteristic. Inside nesting cavity, the Inner spaces and its dimensions are similar for both males and females, but it varies for different species. Egg-laying and immature development is completed inside cells (Joshi *et al.,* 2020); however some studies showed that nesting dimensions and cell structures also vary within the species. But it is assumed that this difference in nesting characteristics within the species is due to some external influence of biotic and abiotic factors. Therefore, in this paper we are discussing the nesting behaviours of wood nesters and nesting substrate features.

Nesting substrate structures and origin

In Ladakh, we observed that in old plants and dead rotten fallen wooden logs there are various factors that make cavities, holes and fishers (**Figure 1 to 12**). The factors such as winds, rainfall, insect pest damage, vertebrate (especially birds) and invertebrate, fungi, bacteria, flooding, cutting of plants, drilling holes, nailing, wood and furniture factories, foresters and farmers contribute to creation of holes, cavities and galleries (Khan, 2020) in woods that are adapted by wasps and bees for nesting and provisioning thereof. Social forestry pests are dominantly comprised of coleopteran borer complexes and belong to various families like, Anodidae, Brentidae, Platypodidae, Scolytidae and Buprestidae. Whileas, the larvae of some Lepidoptera and dipteran results in galleries and cavities in trunk and twigs of dead, damaged, rotten and stressed trees. In tropical forests varying types of structures are created inside wood differing in dimensions and origin. Many times, in forest areas it is found that both live and dead trees are chosen for cavity construction. It is observed that not same species use the cavity always; however, one species create construction and other proliferate in it, for example, fungi.

As far as the origin and availability of cavities are concerned several plant biochemicals and wood textural features are responsible for stimulation of wood nesters (Grunseich *et al.,* 2020). The number of small galleries, cavities and fishers increases with the age of trees; further with aging of the tree the activity of physical and biological agents increases that contributes to the rotting and denaturation of wood. In due course, the plant senescence in the forests meet the equilibrium point, defined by the rate of cavity increase that is recompensed with rate of cavity filling and decrease due to falling and death of trees. Further, the rate of decrease of cavities in deteriorated and rotten wood under natural condition is done by filling due to debris, soil, mosses, litter and organic matter. Generally, the undisturbed forest areas have more standing of dead and rotten trees acting as a source of nesting substrate for diverse types of living organisms (vertebrate, invertebrates, pests and beneficial organisms) including bees and wasps. Under temperate conditions, the forest plants have huge biomass, volume, longer life span, so cooperatively less deterioration due to physical and biological agents. This leads to variability in cavity dimensions, numbers per tree and therefore increases the pressure of animals that are in search of nesting substrate. Forests (temperate areas) subjected to cyclic changes and disturbances due to various biotic and abiotic factors, the availability of cavities should be greater; that is however limited by factors such as intense forest perturbation that reduces the number and nature of cavities and galleries in tress, once the tree die in very young age. The common cyclic disturbance that normally occurs in forest areas includes localized and less intense burning, looping of trees and branches, cutting of small trees, fodder requirements, pollarding, drying and falling under heavy snow fall etc.

Wood physical properties and anatomical characteristics vary widely according to tree species, determined by local ecological conditions such as water availability, and edaphic and climatic factors (Zhao *et al.,* 2020). Under natural conditions some tree species are susceptible to develop cavities and hollows than others. The vibrations is due to degree of resistance to fire, durability, hardness, chemical composition, proneness to gall formation, branching and resistance to physical and biochemical processes that lead to wood rotting and decomposition. Prolong exposure of plants to direct sunlight increases the development of cavities and hollows. These indications showed that these substrates are extremely unstable and can fall by the action of gravity, wind and snow fall. Trees with many cavities and hollows are more prone to the destructive effects of various biotic and abiotic factors.Generally, aged and matured tree goes through successive stages of senescence and proneness to physical decline and at each stage cavities and hollows are produced and are made available for different animal species. Therefore, it is understood that trees of higher age and stages of physical deterioration are utilized and by different organisms for nesting and proliferation. The heavy truck tree species like *Eucalyptus* develop more wood cavities of different dimensions of holes than small-trunk species. Higher trunk diameter tree species of family Caryocaraceae produces more suitable hollows preferable for nesting by eusocial bees *Melipona quadrifasciata*.

Trees provide many benefits to bees and wasps (Patel *et al.,* 2021). Besides providing cavities for nesting they also offer food products such as pollen, nectar, potential preys and useful materials for nest construction such as resins, gums, and oils (e.g. caraboniodae

wasps). Woodencavities and galleries can also house several other organisms (fungi, insects, birds) that are food sources for many species of predicators.
There are many intrinsic and extrinsic factors affect cavity occupation and preference (Szczepko *et al.,* 2020) comprised of kind of cavity (dug or not in trunk or branch), animal size in relation to hollow entrance orifice size, cavity position on the tree and orientation. The other factors which are essential for the reproductive point of view are thermoregulatory capacity, and social organizations certainly influence cavity occupation and use by animals. For invertebrates especially, for insects species of order Hymenoptera the probability of using tree cavities and hollows is positively correlated to the percentage of cortex in trunks, distance between the tree and the source of water or another tree with cavities, orifice entrance angle, and local density of trees, foraging resources, type of forage, diversity of vegetations, competitor species, distance of forage, abiotic factors and anthropogenic pressures. Further, the tree age, diameter and height, liana and epiphyte cover on the tree and cavity height relative to the ground disfavor the probability of cavity occupation and use. Most wood nesters use and occupy preexistent cavities probably make their choices based upon tree species and physical quality of the hollows themselves. Some of the species occupy and use cavities in environments with distinct botanical compositions are similar whileas others are able to use artificial cavities that can be manufactured from timber of different plant species. This indicates that trees are not a factor when choosing the nesting species. However, the data on solitary and social Aculeata nesting in preexisting wood cavities is not conclusive, and more research is need to determine the exact factor of nesting preference. Much of the studies conducted in past about nesting behaviour of various wood dwelling bees and wasps but none of them reach to exact conclusion about their preference, and all failed to make an association between plant species and nesting activity. However the most determining factors when choosing the nesting site can be related to tree structural or architectural traits and to timber physical or chemical properties.Various environmental tend to reduce the availability of nesting sites for wasps and bees. The most adverse are deforestation, fragmentation, burnings, and monocultures all decrease the species' population densities and consequently, their diversity of assemblages. For economic purposes, the forest management and locals' farmers affect the availability of plant species and of natural cavities and hollows, which directly affect the population densities and their habitat. Therefore, these factors affect either mortality caused by the fall of trees during timber exploration or due to lower availability of cavities.

Cavities in wood act as Nest for Solitary Aculeata

Animals especially bees and wasps are in the need of tree cavities for completing their life cycle (Wiebe *et al.*, 2020). Research showed that the females of most species of solitary wasps burrow one or more nests in the soil, whileas other species construct nests attached to vegetation or other substrates, utilizing mud and several plant materials. Wasps and bees are different in relation to nest construction, for example *Trypoxylon politum* female usually construct long, tubular, mud nests but can also nest in tree holes. However, some species are philopatric and females of different and successive generations nest continuously in the same area where they emerged.Nests of solitary wasps are provisioned with immature and adult spiders, insects of other orders, pollen and floral nectar. Many species make their nests by removing pith from the stems and twigs of living and dead plants, or in preexisting cavities in the wood. Females that nest in stems burrow inside to adapt their depth and diameter for the construction and provisioning of cells; therefore wood physical characteristics seem to be preferred.

In insect species that are adapted to preexisting holes and cavities in wood (Powell *et al.*, 2020), lack the burrowing behavior, and adapt to preexisting cavities by remove small chips, wood fragments, and other kinds of materials found blocking the cavity. They strengthen the nest cavity by several means, like compartmentalization through cell wall and partition constructed with different materials. The most common materials used are mud, sand grains, plant resins, small pieces of leaves, petals and grass filaments, fibers, small twigs, threads of spider webs, the female salivary secretions, and even small fragments of insect bodies. These cavities can be found in trunks, twigs of live and dead trees and timber; this nesting behaviour is mostly frequently found among the solitary wasp species belonging to families such as Crabronidae, Sphecidae, Pompilidae, and Vespidae (Eumeninae). The variation in abundance and quality of nesting sites is essential for the maintenance of predatory, solitary wasp populations that depends on the availability of adequate sites for nesting and preying. Like solitary wasps, the huge numbers of solitary bee species having a variety of nesting habits. Generally, the solitary bees construct nest at surface or underneath tree trunks, bushes, litter, termite or ant nests, or even on abandoned nests of other wasp and bee species, differing in dimensions and density compared to solitary wasps nests. It is observed that females of many solitary bee species nest in sites other than those where mating took place; while adults forage at different distances and in varying directions within the range of approximately one or few kilometers. Therefore, knowing and preserving the solitary bee habitats are important for the maintenance of these Aculeata populations in the climate change era.Some bee species nest in offside the twigs and branches, or in preexisting wood cavities and holes, twigs burrow inside to construct their cells and burrow galleries in the hard wood of many tree trunks. Those species which choose preexisting holes and cavities in wood to strengthen their cavity by adding of several materials to their nests, such as sand grains, plant resins and oils, small pieces of leaves and petals, and sawdust. Cavities can be situated in trunks, twigs or branches of live or dead trees and also in buildings, it is due to the reason that some females can reuse the abandoned nests located in wood cavities, a common behavior among the species of Apidae, Megachilidae, and Colletidae.

Wasps and bees form guilds (Odanaka and Rehan, 2020), based on that they are classified according to their offspring and adult food sources and nesting substrates. A guild is a group of species that explore the same resource in a similar way, usually contains species that are not related taxonomically, but explore a similar resource. Further, when a resource is not a food source (e.g. a microhabitat), the term guild is not used and it is said that species belong to different trophic levels. The solitary wasps and bees are best example of nesting guild using preexisting cavities for nest construction, said to be belong to one nesting guild. Further, the Aculeata species that burrow their nests in the ground belong to a different nesting guild based on their food resources and nesting substrate. Biology of the wasps and bees nesting in the soil is better known than for the biology of species that nest in other substrates. The nests in the soil are more easily found and sampling is easy to be done for further evaluation. Generally, the nesting site selection in soils is successful once species considers factors such as soil topography, groundcover vegetation, edaphic and microclimatic characteristics. The most primitive group among all insect nesters are soil dwelling bees, whileas the above ground nesting behavior were raised in Apidae, Megachilidae, Hylaeinae and Xylocopinae. This showed that nesting behaviors vary widely among families supported by an evolutionary derived condition; for example, females of several Crabronidae and Sphecidae species nest in preexisting wood cavities or in plant twigs and branches.

Bee traits associated with nesting behaviour are favored by natural selection (van Alphen and Fernhout, 2020) also parallel to this is that reproductive success among the solitary wasp (Crabronidae) is a function of female size and soil physical properties. For example, in case of nesting site with harder soils, females are more aggressive toward their conspecifics. Therefore, it exhibited that soil hardness represents a selective pressure for female with larger bodies, which can enhance fitness of bigger females during agonistic encounters. Some species (*Hylaeus grossus*) are apomorphic means that females often leave an exceptionally large empty space useless, showed that branch cavities are not a limited resource. Aculeata usually form a liner series of cells separated by partitions, whileas in some species partitions are absent. Cell density in nest varies with species; whileas in some species empty spaces at the end or in middle of liner cell series of provisioned cells are found called as vestibular and intercalary cells. The function of the empty space is to prevent egg and immature predation and parasitism by natural enemies.

Insects which nest in wood have less nesting sites and are comparatively less fertile (Dufour-Pelletier *et al.,* 2020). Wood nesters have limited and rarer nesting substrate; found among species that build their nests in preexisting wood cavities than among species that dig the soil. Factors that determine the success of the nesting by solitary Aculeata species in preexisting cavities includes: availability of suitable cavities, female size, distance between nesting site and food source and availability of nest-building materials, as perquisite for successful and rich bio-diversity of these species in any habitat. The availability of materials is determined by, cavities in wood, sawdust, and small chips of wood. The species *Centris fabricius* are unable to dig in the wood and rely mostly on boring wood insects to build the nests and their activities are highly dependent on quality of wood, which can be the main reason for the Aculeate species to nest primarily in preexisting holes in human-made environments, where cavities are not due to the action of boring insects.The great amount of leaf fragments found in bee nests of the genus *Megachile latreille* suggests that females bring them from nearby areas, with physical structure and chemical composition of these leaf fragments are of fundamental importance for nesting success. Saponines present in the leaves of some plant species causes larval mortality in *Megachile rotundata* (Fabricius), which is further supported by the features that the leaves differ in toughness, and nesting females may need to press their mandibles strongly, to properly cut the leaves to be used for cell construction. This suggested that not all the leaves are structurally or chemically suitable for cell construction by megachilid bees and cannot guarantee nesting success. The nesting size in cavity nesters influences the number of cells constructed by females and that cell size affects sex ratio, fitness, no of eggs laid and abundance of species in environment. For bees and wasps, the nesting behavior and mating sites vary widely, for example the carbonid wasp *Trypoxylon* of sub-genus *Trypargilum* mate near or inside their own nests, located in preexisting cavities in wood. Males guard the nest against intruders and assist nesting females in storing preys in the nests. Males of carbonid wasp species *Trypoxylon*search actively for empty cavities or follow the conspecifics nesting females to a cavity; whiles as females search for nesting materials and prey upon spiders whereas males defend the nest against usurpation by other non-specifics nesting female wasps or males, or against parasites and predators. Once female return to their nests, they copulate several times, and female lays eggs only when the cell contains enough preys; that (preys) are place and arranged in the cells by males. Generally for Aculeata species male parental care is not common among, as an important evolutionary trait in increasing male and female fitness, thus guaranteeing male paternity.

In Aculeata species the haplodiploidy is important (Gadallah *et al.,* 2020), nest guarding behavior and the copulations in the nest can indirectly increment female production, sex being genetically related to the male; this makes it possible when females allocate more time and become more efficient in foraging while the males protect their nests. Females of crabronid wasp species *Trypoxylon latreille* exert a strong sexual selection pressure on males; therefore reproductive success of this wasp species depends not only on cavity and food availability, but also on the existence of nest-guarding males. Males are reported to guard nesting cavities, produced in small cells provisioned with a small amount of food, ovules (n) will preferably be placed in cells with small amount of food, thus increasing the chances for raising male individuals, as opposed to eggs (2n), which would raise female individuals.

		
Figure 1: Old dead wooden logs of populous with nesting holes made by *Xylocopa* spp.	**Figure 2:** Wooden logs of Robinia spp. with nesting holes made by *Xylocopa* spp.	**Figure 3**: Reed nest inhibited by wild bees, cells and larvae partitioned by cell walls.
		
Figure 4: Flat head borer infested peach tree, the galleries are later inhibited by wild bee spp.	**Figure 5:** Dead wooden logs used by bees for nesting	**Figure 6:** Dead wooden logs of willow used by bees (Megachile) for nesting
		
Figure 7: Leaf bits cut from willow by Megachile spp. used for strengthining the nesting cavity	**Figure 8:** Willow fowers used for foraging by wild bees	**Figure 9:** Flat head borer infested cherry tree, the galleries are later inhibited by bee spp.
		
Figure 10: Populous tree logs (dead logs) not attacked by any borer species due to less temperature, inhibiting microbial decomposition of wood. No borer damage occurred.	**Figure 11**: Populous tree logs (dead logs) on direct contact with soil and grass, extremes of low temperature ceased the enzymatic activity thereof the microbial decomposition	**Figure 12:** Populous tree logs (dead logs) surfaces look fine, shining and damage less; the extremes of low temperature ceased the enzymatic activity thereof the microbial decomposition

Figures showing dead wooden logs (insect pest infested/un-infested) in fields of Ladakh as a source of nesting substrate for various bee and wasp species [2019-2021].

Dead wood cavities and nesting habitat for species other than Aculeata

It is observed that many vertebrate and invertebrate animal species use preexisting holes and cavities in wood for nesting and other activities (Frey *et al.,* 2020). Orthoptera (20%) and Hymenoptera (10%) are dominant in occupying nesting cavities and a two year monitoring showed that occupation of artificial cavities is strongly correlated with occupation of natural cavities by hymenopteran species. The microhabitats in decomposing trees and trunks is an evolutionary behavior for several groups of insects, this (microhabitat) feature in wood stimulates bees and wasps for nesting, as the maintenance of a suitable microclimate is important for the development of Aculeate offspring nesting in wood cavities. Among many wood nesters, only the eusocial wasps and bees are able to exert thermoregulation in their nests; unlike of solitary Aculeata which prefer to nest in suitable cavities, with more or less insulation to resist climatic variations.

Biological decomposition of wood at Ladakh region

Under extremes of low temperature the decomposition of wood in Ladakh region is very less. Biological decomposition of wood is an important (Goodell *et al.,* 2020; Mattila *et al.,* 2020) part of the carbon cycle of nature, caused by fungi, insects (pests and beneficial insects), and marine borers that use the wood as food or shelter, or both. Due to low temperature the microbial growth and proliferation and the enzymatic activities are very less that determines that wood decomposition and availability of nesting sites and hollows for insect pollinators are less.

Table 1: Mean nest density (holes/m^2) in woody plants at Ladakh and insect families [2019-2021]

Tree species	No. holes in occupied by bees/wasps (%)/m^2	No. of live nesting cavities /m^2 (current year)	No. dead/ abandoned nesting cavities/m^2 (previous year)	Nest height from breast height (m)	No. cells at or below breast height	Bee/wasp Species inhibiting the cavity
Apple	10	5	4	1-3	6.5-6.98	Vespoidea, Apoidea, Megachilidae
Willow	20	8	3	4-7	5-7	-do-
Populous	8	3	2	6-8	8.5-9.04	-do-
Walnut	2	4	1	3-20	6.78	Vespoidae, Megachilidae
Apricot	12	3	2	2-3	6.50	Vespoidea, Apoidea, Megachilidae
Peach	2	0	1	1-1.3	5.01	Vespoidae, apoidae
Sea-buck thorn	0	0	0	0	0	NA
Wild reeds	1	0	1	-	0	Vespoidae, Megachilidae
Robinia spp.	1	1	1	3-12	4.67	Vespoidae, apoidae , Megachilidae

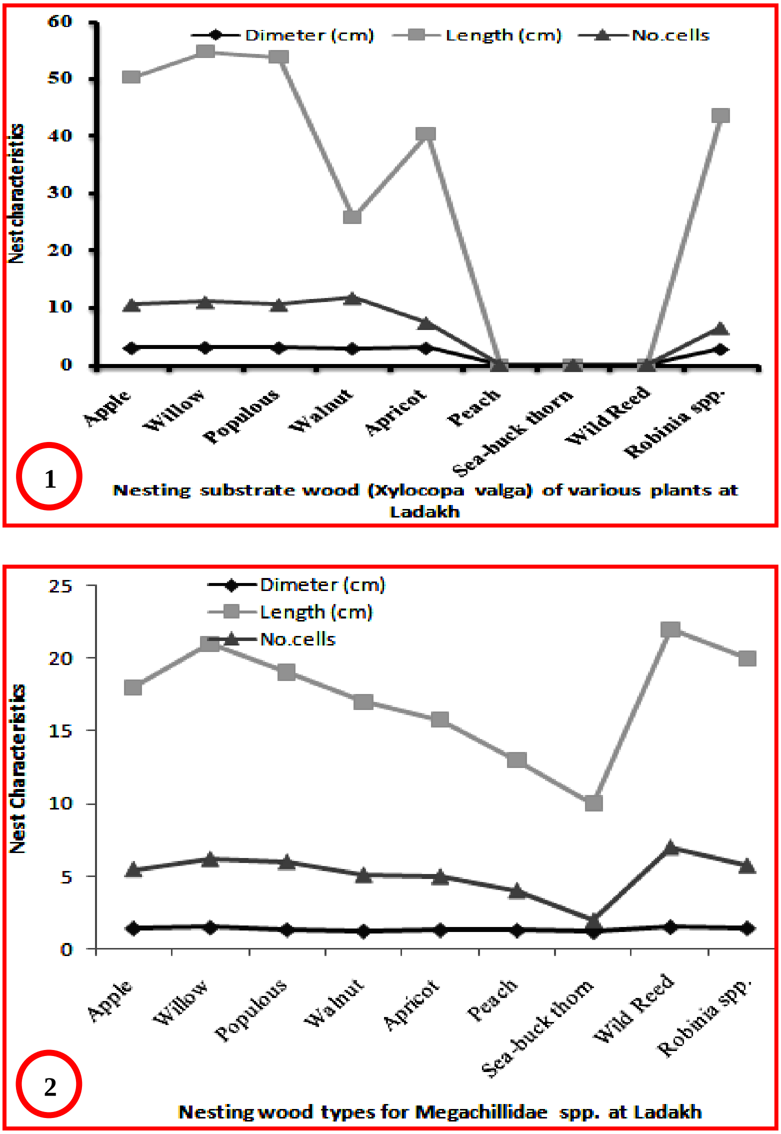

Figure 1 & 2: Nesting behaviour of *Xylocopa Valga* and *Megachilidae* species at Ladakh region

The lesser availability of nesting sites and substrate has a direct impact on pollinator diversity at Ladakh region. Biochemically, in wood the lignin provides a physical barrier to enzymatic decomposition of cellulose and hemicelluloses, which is breached mechanically by insects and marine borers, through white- and soft-rot fungi, and possibly by small non-enzyme catalysts in the case of brown-rot fungi. In wood, temperature plays an important role in biological and chemical decomposition. Generally, the enzymes endo- and exo-glucanases and β-glucosidases decompose cellulose, endo-glycanases and glycosidases degraded hemicelluloses and most of nonspecific enzymes, non-enzymatic, oxidative agents degrade lignin in wood.

The brown rot fungi (Bari *et al.,* 2020) cause rapid loss in wood strength (Zhou *et al.,* 2020) however; the application (biological pulping, pretreatment for enzymatic conversion of wood to sugars) of wood-decomposing fungi is limited currently to production of edible mushrooms. Further, the susceptibility of wood cell wall polymers to biological decomposition is determined largely by their accessibility to enzymes and other metabolites produced by wood-destroying fungi or insects and marine borers; especially through microorganisms that live in the digestive tracts of these animals. The decomposing microbial populations in cold arid regions are very less, so the wood remains un-decomposed for years after drying or after prolongs exposure to moisture under harsh winters. The direct physical contact between the enzymes or other metabolites and the wood cell wall polymers is prerequisite to hydrolytic or oxidative degradation, because cellulose, hemicelluloses, and lignin are all water-insoluble polymers and are deposited in wood cell walls in intimate physical admixture with each other. This necessary physical contact can be achieved only by diffusion of the enzymes or other metabolites into this complex matrix or by fine grinding of the wood prior to digestion, with a crucial structural component as lignin that increases the biological decomposability. The cellulose microfibrils are coated or over layered by hemicelluloses which in turn are under a lignin sheath covalently bonded to some extent, physically intermixed with hemicelluloses. The bonding between lignin and hemicelluloses are probably infrequent. The digestibility of solid wood and other intact lignified tissues (lignocelluloses) is largely a function of lignin content, which support the biological mechanisms evolved for overcoming the lignin barrier. The insects and borers physically disrupt the barrier by grinding the wood very finely (mechano-biochemical decomposition); whileas the microorganisms, primarily higher fungi, decompose lignin and thus expose the polysaccharides (biochemical decomposition). The lesser coleopteran diversity and in other words lesser infestation of hard wood borer in Ladakh is an indication of poor wood decomposition. The fungi apparently secrete non-enzymatic cellulose-depolymerizing agents that penetrate the-lignin sheath and cause degradation thereof; however in Ladakh region due to harsh climatic conditions decomposing fungi population are lesser that impacts directly the availability of nesting structures for the insect pollinators. This is one of the reasons for lesser insect diversity at Ladakh region.

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