

**PLANT-FRUGIVORE INTERACTION AND
SEED DISPERSAL SYNDROMES
IN SHOLA FORESTS OF
THE WESTERN GHATS, INDIA**

Thesis submitted to the University of Calicut in partial fulfillment of the
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CERTIFICATE

This is to certify that the thesis entitled "PLANT-FRUGIVORE INTERACTION AND SEED DISPERSAL SYNDROMES IN SHOLA FORESTS OF THE WESTERN GHATS, INDIA " is an authentic record of research work carried out by Ms. Nimisha E.S. under my supervision and guidance in the Forest Botany Department of KSCSTE- Kerala Forest Research Institute, in partial-fulfilment of the requirements for the degree of Doctor of Philosophy of the University of Calicut. This has not been previously submitted for the award of any degree, diploma, associateship or other similar titles to any candidate of any university.

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DECLARATION

I do hereby declare that the thesis entitled PLANT-FRUGIVORE INTERACTION AND SEED DISPERSAL SYNDROMES OF TREES IN SHOLA FORESTS OF THE WESTERN GHATS, INDIA submitted to University of Calicut for the award of DOCTOR OF PHILOSOPHY IN BOTANY (Faculty of Science) included the data generated by the original research by me under the supervision and guidance of Dr. V B Sreekumar, Scientist Kerala Forest Research Institute, Peechi, Thrissur. The work has not been submitted to any University or Institutions for the award of any degree. The particulars given in the thesis are true to the best of my knowledge. I further declare that the findings of this research contribute in general to the advancement of knowledge in science and in particular to the Shola forests of Kerala portion of Western Ghats.

Place: Peechi

Date: 12-09-2025



Nimisha E.S

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ABSTRACT

The Shola forests of the Western Ghats are ecologically rich, harboring a range of plant-animal interactions that are essential for maintaining the unique biodiversity in this ecosystem. Seed dispersal by frugivores is an essential process that influences forest regeneration, affects species diversity, and community composition. This thesis explores seed dispersal dynamics in Eravikulam National Park, examining how plant diaspore traits, frugivore feeding patterns, fruit production, and abiotic factors such as altitude and climate collectively function to shape dispersal processes in this tropical montane ecosystem. Diaspore morphology, including fruit pulp type, color, size, and seed size, is a key factor in determining the dispersal mechanism, with findings revealing that brightly colored, fleshy fruits are primarily dispersed by birds, whereas lighter seeds are more effectively dispersed by wind. By studying 105 tree species across 25 Shola forest patches, this study highlights how specific traits promote or limit seed dispersal which in turn contribute to forest structure and resilience.

Detailed observations of frugivore interactions with fleshy fruits illustrated a substantial dietary overlap between species, highlighting a complex web of interactions between species. Frugivores such as birds in the Pycnonotidae and Sturnidae families and mammals such as langurs, civets, and squirrels were found to be particularly influential, with larger frugivores predominantly consuming larger fruits and playing a key role in dispersing seeds of greater size, which often support seedlings with higher survival rates. Transect walks, camera traps, and fecal analysis were used to gather data for the construction of quantitative seed dispersal networks, which highlighted the ecological importance of frugivores with high species strength and interaction asymmetry, which frequently render them irreplaceable dispersers within the community.

Rainfall and minimum temperature were strongly associated with seasonal fluctuations in fruit biomass production, with fruit production reaching its maximum during the wettest months. This seasonal fruiting pattern aligns with the "germination hypothesis," which posits that fruiting during the rainy season enhances seed germination success, and provides crucial food resources for a diverse community of frugivores. Across three years, fruit biomass averaged 384.69 kg/ha/year, comparable to other tropical montane ecosystems. A considerable amount of this biomass was made up of larger fruits that were dispersed by both mammalian frugivores and birds like Nilgiri wood pigeons.

The final analysis explored how environmental gradients and abiotic factors drive frugivory, seed dispersal, and co-evolutionary dynamics within the Shola ecosystem. A study of 44 forest patches, each varying in altitude (1690–2024 m) and size, revealed that frugivore density peaked at lower elevations, where larger fruiting trees were more prevalent, while smaller frugivores predominated at higher altitudes. Correlations between body size, gape width, and fruit traits showed that large frugivores consume larger fruits, aiding the dispersal of seeds that benefit from more extensive dispersal distances at lower elevations. The findings suggested that as altitude rises, environmental constraints cause smaller, lighter fruits to be adapted to dispersal by smaller-bodied frugivores and by abiotic factors like wind. Abiotic factors like temperature and rainfall were found to have a significant impact on both frugivore abundance and fruiting phenology.

In conclusion, this thesis offers a comprehensive understanding of how fruit characteristics and frugivores are highly adapted to the conditions found in Shola forests. These results highlight how diaspore characteristics have evolved to optimize seed dispersal, often in response to abiotic gradients and through specialized interactions with specific dispersers. This study provides important insights into conservation biology by highlighting the importance of preserving habitat connectivity and protecting diverse frugivore assemblages to promote effective seed dispersal and forest regeneration, particularly in tropical montane forests where environmental change and habitat fragmentation are becoming a growing problem.

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Introduction



Figure 1.1 Shola forests of Eravikulam National Park

The forest is not a resource for us, it is life itself. It is the only place for us to live.

— *Evaristo Nugkuag Ikanan*

1.1 | Shola forests

Tropical montane forests (also tropical montane cloud forests or cloud forests) harbor great diversity but are threatened by climate change and conversion to other uses, such as agriculture and plantations. This ecosystem has adapted to the high frequency of cloud-water extraction and immersion. Global air masses are filtered by this ecosystem in a manner that allows them to absorb and incorporate nutrients and water from fog and mist into their cycles. These are forests above 1500 m asl, but may occur as low as 500-800m asl closer to the coast (Bruijnzeel and Veneklaas, 1998; Hamilton 1998; Scatena et al., 2010). According to Bruijnzeel and Hamilton (2000), there are five types of tropical montane forests (TMF). Four of these were classified according to elevation and tree height: subalpine cloud forest, upper montane cloud forest, lower montane forest, and

lower montane cloud forest. The fifth type is a low-elevation azonal dwarf cloud forest. Many tropical regions are located in these forests, including Central and South America (including Ecuador, Mexico, Venezuela, Colombia, Cuba, Jamaica, British Guyana, and Costa Rica), Tropical Africa (particularly Cameroon, Uganda, Madagascar, and Tanzania), and Tropical Asia (South India, Sri Lanka, Laos, Borneo, New Guinea, Malesia, Thailand, and Vietnam) (Gentry, 1992). In tropical montane forests, the two main environmental gradients affecting tree species composition are altitude and terrain (Homeier et al., 2010). Key variables, such as temperature, precipitation, wind, cloud cover, and soil fertility, showed consistent fluctuations along altitudinal gradients.

In tropical montane forests, increasing elevation is associated with a reduction in tree height, an increase in leaf thickness, and greater complexity in tree architecture. TMF is also distinguished by the prolific growth of epiphytes and mosses as well as a lack of pronounced vertical stratification. The soils in these forests are typically clay-rich, acidic (low pH), high in organic matter, and often nutrient poor. TMF exhibits high levels of endemism largely because of the limited availability of suitable habitats (Bubb et al., 2004). Situated in the headwater catchments of seasonal or perennial streams, these forests provide critical yet often underappreciated ecosystem services to downstream communities.

In the Western Ghats-Sri Lanka (WGSL) biodiversity hotspot (Myers et al., 2000), tropical montane forests occur as a mosaic of forest patches, locally referred to as Sholas, interspersed in valleys between rolling grasslands above 1500 m. This distinctive landscape is commonly known as the Shola-grassland ecosystem. Foresters such as Champion and Seth (1968) equated Shola forests with "stunted forests of the high-elevation belts" and classified them under the category of Southern Montane Wet Temperate Forests (Subgroup: IIA - Type C1), typically found at elevations above 1500 m.

In Kerala, typical Shola forests are found along the crests of the Western Ghats, at elevations above 1800 m. Notable regions include Eravikulam in Idukki, Devarmala in Pathanamthitta, Agasthyamala in Thiruvananthapuram, Sispara Ghat in Palakkad, New Amarambalam in Malappuram, Vellarimala in Kozhikode, and the Brahmagiri Hills in Wayanad. Many of these areas are extensions of forest types from Tamil Nadu, including the Nilgiris and the Anamalai Hills. The majority of Kerala's Shola forests, including the

largest, Mannavan Shola, are concentrated in the Idukki district, covering approximately 70 km² (CESS, 1984).

Similar to other TMFs, Shola forests are characterized by stunted, profusely branched trees with umbrella-shaped canopies and crooked branches densely covered in epiphytic mosses, ferns, lichens, and orchids. Shola forests are often called living fossils due to their inability to expand under current climatic conditions. Morning frost and sun prevent saplings from surviving in grasslands, particularly on eastern and southern slopes. While woody species in grasslands are cold resistant and extend to higher altitudes, predominantly tropical species within the Sholas cannot survive in the open. However, stable temperatures inside Sholas allow for successful regeneration, as studies have shown that the balance between Sholas and grasslands fluctuates over geological time. The stunted growth of Shola trees is an adaptation to resist damage from strong winds, which makes windfalls rare. The hill folds and depressions, where the Sholas are located, provide further protection.

In open grasslands, winter frosts can lower temperatures below 0°C, whereas they remain above freezing inside Sholas (Ranganathan, 1938). Frost causes intracellular crystallization in plants and rapid thawing from the hot morning sun leads to rapid transpiration. Frozen soil prevents water absorption, causing water stress and physiological dryness, leading to wilting and death, particularly in seedlings with shallow roots. However, established trees survive with minimal damage. Regeneration inside Sholas is strong because of minimal frost damage (Jose et al., 1994); however, seedling mortality is high in winter because of low temperatures and moisture stress (Khan et al., 1986). Most tree species belong to the Lauraceae, Myrtaceae, Rubiaceae, and Oleaceae families, and bear drupaceous, recalcitrant fruits with short seed viability (Kumar and Chacko, 1999). These seeds, which are shed with high moisture content, are highly susceptible to desiccation and chilling, shortening their viability to a few weeks or months, depending on the species (Farrant et al., 1988). Very few studies have quantified biomass production in Sholas. According to phytogeographical studies, genera found on the edges of Shola patches or as lone trees in grasslands are usually subtropical or temperate, with some Himalayan species including Mahonia, Berberis, and Rhododendron. The majority of species found in the Shola fragments are Indo-Malayan or Indian in origin (Suresh and Sukumar 1999; Nair and Menon 2001).

Early descriptions viewed it as a dual climax ecosystem (Ranganathan 1938), whereas others argued for a single climax, either biotic (Bor 1938; Noble 1967) or edaphic (Jose et al., 1994). The $\delta^{13}\text{C}$ analysis of peat samples from Nilgiris revealed cyclical shifts in the vegetation cover. Arid conditions from 20,000 to 16,000 yr BP favored C4 vegetation, followed by a wetter phase at approximately 11,000 yr BP, which promoted C3 vegetation. A weaker monsoon around 6,000 years BP led to C4 expansion, with brief warm, wet conditions around 600-700 years BP (Sukumar et al., 1993). Fire, frost, and wind are key factors that influence the Shola distribution. Fires, often man-made, begin in settlements and spread to grasslands, sometimes reaching Sholas through reed zones. These fires destroy seedlings that survive the winter frost in grasslands, thereby hindering the expansion of Shola. In some cases, fires are deliberately set to allow fertile ash from grasslands to reach cultivated land during rains.

Abiotic factors, such as altitude and patch size, also play important roles in the ecology of the Shola ecosystem. Species diversity tends to be the highest at lower elevations and decreases with increasing altitude (Thomas et al., 2011). Large Shola patches provide frost-free interiors that preserve tropical lineages (Das and Ratnam, 2022). Forest composition, species richness, density, and distribution can be affected by habitat disturbance (Mohandass et al., 2016). Conservation efforts should focus on large undisturbed Shola forest patches to preserve their diversity and species of conservation importance (Nair and Menon, 2000). Studies have demonstrated the significance of abiotic factors such as rainfall and temperature on phenological patterns across different forest ecosystems in India (Krishnan, 2002; Nanda et al., 2014). However, few studies on phenological patterns have been conducted in Shola forests.

Research conducted on other montane ecosystems has shown that Shola forests are closely linked to seasonal rainfall. In Sholas, fruiting peaked during months of high rainfall availability, while leaf flushing and flowering events occurred during the dry season and early calendar years (Jeevith and Kunhikannan, 2019; Sellamuthu and Lalitha, 2010).

Numerous wildlife species of conservation significance, such as the tiger (*Panthera tigris tigris*), Nilgiri langur (*Semnopithecus johnii*), gaur (*Bos gaurus gaurus*), dhole (*Cuon alpinus*), and Nilgiri marten (*Martes gwatkinsii*), find home in the Shola-grassland ecosystem mosaic. The avian community in Shola exhibit strong habitat selection patterns. Species endemic to Shola include Nilgiri pipit (*Anthus nilghiriensis*) and black and orange

flycatcher (*Ficedula nigrorufa*). Ongoing investigations have been conducted on amphibians, birds, invertebrates, and fish in the Shola forests of Western Ghats (Dinesh et al., 2008; see also Nair et al., 2001). However, aside from the Nilgiri Tahr, there is a limited body of scientific literature concerning faunal species in the Shola grassland ecosystem mosaic.

1.2 | Frugivory and seed dispersal

Pollination and seed dispersal are examples of animal-plant mutualism that are essential ecological processes in many ecosystems worldwide (Herrera and Pellmyr, 2002). Seed dispersal, a key ecological process for forest regeneration and recruitment, is vital for maintaining biodiversity and restoring degraded lands (Jordano, 2000; McConkey et al., 2012). The ability of plants to move is largely limited to the dispersal of pollen and seeds, and seed dispersal allows plants to explore and colonize new competition-free habitats, aid in the regeneration of plant populations, promote gene flow, and ultimately help maintain plant diversity (Howe and Smallwood, 1982; Connell and Green, 2000; Ehrlén et al., 2006). Seeds can be dispersed by multiple non-exclusive mechanisms, often classified as biotic or abiotic, depending on whether they contain animal vectors. In the tropics and subtropics, fruit-eating animals and birds (frugivores) are vital dispersers of many plants, with some plant species being dispersed by others (Jordano, 2000). These mutualisms involve reciprocal benefits, and many animal species depend critically on the use of fleshy fruits or seeds as food resources. Fruit characteristics, such as size, morphology, nutritional quality, and ripening time, can influence disperser choice and dispersal effectiveness (Willson and Traveset, 2000). Animals also have morphological adaptations that aid in seed dispersal. Common morphological, physiological, and phenological characteristics are associated with particular types of dispersal agents and are referred to as ‘dispersal syndromes’ (Renner, 1987; van der Pijl, 1982). Understanding dispersal syndromes is crucial for predicting the responses of plant species to environmental changes, managing ecosystems, promoting forest regeneration, and conserving biodiversity, particularly in fragmented or degraded habitats where natural seed dispersal dynamics are disrupted. Based on differences in body size, diet, and behavior, frugivores differ in the quality of the fruits they consume and the spatial locations in which they carry seeds within a landscape.

In the tropics and subtropics, where most plants are dispersed by animals, identifying the spatial drivers and patterns of dispersal requires an understanding of the ecology of seed dispersers (Westcott et al., 2005; Russo et al., 2006). As several dispersers may interact collectively with the same plant species and in complex networks (Bascompte et al., 2003; Donatti et al., 2011), it is essential to study these interaction networks to gain a better understanding of seed dispersal at the plant and disperser community levels. Understanding the roles of endemic and at-risk species further highlights the importance of this network-level study.

The maturation of fruits of a particular dispersal syndrome has been reported to coincide with suitable conditions (biotic or abiotic) for seed dispersal in the tropics (Frankie et al., 1974; Smythe, 1970; Wilkander, 1984). Abiotic factors, such as seasonality, expose plants to periodic changes in resource quality and availability (Fretwell, 1972). Most tropical environments experience seasonal variations in temperature, rainfall, and wind speed. In the tropics, zoochorous species are more common during rainy seasons and anemochorous species are more common during dry periods (Griz and Machado, 2001; Escobar et al., 2018). For plant communities to optimize resource consumption by animals, phenological patterns play a vital role in promoting physiological and morphological adaptations in plants (Selwyn and Parthasarathy, 2006). These plant adaptations aimed at enhancing seed dispersal, with fruit ripening timed to coincide with suitable environmental conditions optimize the dispersal process (Jara-Guerrero et al., 2011). Despite their significance, the phenological patterns of seed dispersal in tropical montane forests in the Western Ghats are still not well understood.

Seed removal and long-distance dispersal, are often affected by fruit production. Higher fruit production results in greater dispersal, especially when large frugivores such as bears are involved in fruit consumption and seed dispersal (Koike et al., 2022). Quantifying fruit biomass production is essential for understanding seed dispersal associated with different seed dispersal syndromes because it provides information on the resources available for dispersers and the potential of seed for dispersing within ecosystems. The interaction between fruiting trees and seed dispersers is complex, and multiple years of tree observations with varying fruit production are essential to completely understand the seed dispersal process.

Abiotic factors, such as elevation and Shola patch size, affect seed dispersal along with the influence of fruiting phenology. Elevational variations and floristic composition can impact dispersal syndromes and processes. A study on *Schleichera oleosa* (Lour.) Oken found that fruits and seeds from lower elevations (250-500m) were noticeably larger and heavier, with higher germination rates and more vigorous seedlings (Rawat et al., 2020). Fruit size may be subject to selection pressure on frugivores or vice versa, where fruit size may determine the structure of the frugivore guild. In this case, it is difficult to determine the direction of the selection. Correa et al. (2015) and Jordano (1995), contend that frugivores select for diaspore size because gape width and body size limit the size of fruit that a frugivore can swallow (Moermond and Denslow 1985, Wheelwright 1985). Another well-documented trend is a change in the relative proportion of dispersal syndromes with increasing altitude. For example, Grubb and Stevens (1985) found that the proportion of anemochorous species in New Guinea forests increased from 7% (lower montane) to 13% (upper montane), and to 20% (subalpine). Similarly, patch size may result in altered plant-frugivore interactions. The reduced diversity of frugivores in smaller patches can cause over-reliance on generalist species, which may not be as effective in dispersing certain plant species adapted to more specialized dispersers.

1.3 | Threats to Shola forests and seed dispersal mechanism

The Shola-grassland ecosystem mosaic has experienced extensive habitat degradation owing to numerous human interventions. Exotic tree plantations, to increase timber production, were established as early as 1843 (Palanna, 1996) and expanded under colonial rule, particularly in the Palni Hills (Srivastava, 2001), followed by large-scale tea plantations. Invasive shrubs and herbs, such as *Eupatorium glandulosum* and *Cytisus scoparius*, were identified by early researchers (Bor, 1938; Agarwal, 1961) and have continued to expand with new species (e.g., *Calceolaria mexicana* and *Erigeron mucronatum*) (Seshan, 2006). Present-day threats include harvesting Shola species for biomass and fuelwood, as well as cattle grazing, particularly near settlements, which affects species richness and dominance (Chandrasekhara et al., 2001). The Western Ghats-Sri Lanka biodiversity hotspot faces potential extinction due to habitat fragmentation (Brooks et al., 2002), and tropical montane forests (TMF) suffer higher annual habitat loss globally than other tropical biomes (FAO, 1993). In addition, climate change is expected to alter the equilibrium between forests and grasslands, reducing frost and strengthening monsoons, which could favor C3 species (Sukumar et al., 1995).

Numerous threats to frugivores and seed dispersers can seriously disrupt the seed dispersal processes and forest regeneration. Habitat loss and fragmentation are among the most critical threats, which lowers the number of plant and animal dispersers (Wright et al., 2007). The available habitat for frugivores such as birds, bats, and primates is limited by habitat fragmentation and degradation (Kissling et al., 2012). Large-bodied frugivores are threatened by hunting and poaching. The loss of large frugivores can result in reduced seed dispersal distances and altered plant community distributions (Effiom et al., 2013). Climate change intensifies these vulnerabilities by affecting the distribution and foraging behavior of frugivores (Magrach et al., 2014). Invasive species weaken the regeneration capacity of forests by disrupting mutualistic relationships between native plants and dispersers (Aslan et al., 2013). To conserve the biodiversity and ecological functions of tropical montane forests, the above-mentioned risks must be addressed effectively.

The Shola ecosystem richness and forest regeneration depend heavily on complex plant-frugivore interactions during the seed dispersal process. These high-elevation structures are perfect systems for understanding the interplay between biotic and abiotic factors that influence seed dispersal. By focusing on the seasonal availability of fruits and the abundance of frugivores and dispersers in Shola forests, this study sought to present a detailed description of the seed dispersal mechanisms. In this study, we investigated the effects of climate, patch size, and altitude on frugivory, seed dispersal, and plant-animal coevolution. By focusing on the ecological roles of frugivores and the seed dispersal process, this study aimed to support the conservation and restoration of the Shola ecosystem.

1.4 | Scope of the study

This study included a detailed investigation of seed dispersal syndromes and the function of frugivores in maintaining ecosystem resilience in the Shola forests of the Western Ghats. This study explores the seasonality of fruit availability and frugivore assemblages. This accounts for the impact of abiotic variables, including patch size, elevation, temperature, and rainfall. The large number of endemic species present in Shola depends on ecosystem services provided by frugivores for their existence (Myers et al., 2000). Another objective of this study was to evaluate the co-evolutionary relationships and plant and frugivore trait adaptation to gain insight into how plants and frugivores evolved to enhance seed dispersal to suitable microhabitats. The results of this study emphasize how

anthropogenic activities and changing climatic conditions affect seed dispersal networks. Laurance et al. (2011) state that this is crucial in ecosystems that are under the threat of fragmentation since changed dispersal leads to disturbed plant regeneration and limited biodiversity. Studies focusing on Shola forests align with broader efforts to preserve tropical montane forests in the face of habitat loss and continuous climate change (Corlett 2017).

1.5 | Objectives of the study

1. To undertake a detailed account of seed dispersal syndromes, the seasonal availability of fruits produced and abundances of frugivores and seed dispersers in Shola forests
2. To study the effect of various abiotic factors affecting frugivory, seed dispersal, plant-frugivore co-evolution and morphological adaptation in Sholas

1.6 | Organisation of the thesis

This thesis is organized into four chapters with an abstract, introduction, and review of the literature. Each chapter focuses on different aspects of plant-frugivore interactions and seed dispersal in the Western Ghats' Shola forests. The primary goal of this thesis was to investigate how diaspore characteristics, frugivores, and abiotic variables interact to influence seed dispersal and forest regeneration in this unique montane ecosystem.

The first chapter examined the association between various dispersal strategies in Shola forests and diaspore traits, such as fruit pulp, fruit type, color, and size. It focuses on 105 tree species spread throughout 25 forest patches using field observations and field studies over three years. Statistical analyses were performed to understand how diaspore characteristics affect the effectiveness of different dispersal mechanisms. The foundation for understanding how specialized dispersal syndromes affect forest regeneration and biodiversity is laid out in this chapter.

The second chapter examines the significance of frugivores in seed dispersal and their dietary relationships. Using methods such as fecal analysis, camera traps, and direct observation, this study investigated frugivore populations and ingested fruit species. This chapter describes the construction of a quantitative seed dispersal network, focusing on the significant roles of frugivores in preserving plant diversity. The results of this study

highlight the importance of conserving frugivores, particularly during periods of declining frugivore populations.

The third chapter focuses on the seasonal patterns of fruit production and seed dispersal syndromes. By quantifying fruit biomass over three years and analyzing fruiting phenology, this chapter demonstrates how seasonal factors such as rainfall and minimum and maximum temperatures influence fruit availability. This study provides details regarding the timing of fruiting and its importance in supporting frugivores by providing food resources for consumption.

The final chapter investigates the association of abiotic factors such as elevation, temperature, and rainfall with frugivore assemblages and fruit morphological adaptations. This study covered 44 forest patches across a wide range of altitudes. This study examined how frugivores and plant characteristics vary with environmental gradient. Analysis of fruit traits with frugivore morphology, such as body mass and gape width, provides information about plant-frugivore co-evolution and the adaptive processes that affect seed dispersal. This chapter also demonstrates that altitude has a major impact on fruit size, frugivore body size, and dispersal mechanisms.

1.7 | References

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Review of literature

2.1 | Shola forests in the Western Ghats

Tropical Montane Forests (TMFs), often referred to as “cloud forests”, are highly elevation ecosystem that is rich in endemic species, and have unique climatic conditions such as persistent cloud cover. The trees are short, twisted, and multistemmed. Forests have luxuriant epiphytic growth, low above-ground production, low leaf nutrient concentrations, high root-to-shoot ratios, large stem diameter-to-height ratios, and small, thick leaves (Fahey et al., 2015). Globally distributed across regions such as the Andes, the Eastern Arc Mountains, and parts of Southeast Asia, these ecosystems serve as biodiversity reservoirs and climatic buffers (Rodríguez-Echeverry and Leiton, 2021).

Tropical montane forests in the Western Ghats are locally known as **Shola**. The high elevation of these mountain forests is often greater than 1500-1800 m above sea level. They were found in the valleys interspersed between grasslands, resulting in a mosaic of forest and grassland. These forest grassland ecosystems are known as **Shola grassland ecosystems** (Sabu et al., 2011; Sasmitha et al., 2021). Nilgiri Hills and other high-elevation areas of the Western Ghats are the main geographic locations for Shola forests in southern India. In addition to their important roles in hydrology and biogeochemistry, these ecosystems are home to a variety of floral and faunal species of conservation importance (Mohandass and Davidar, 2009). The composition of Shola species changes along altitudinal gradients, with certain species being common at some elevations (Thomas et al., 2011).

Despite their ecological importance, Shola ecosystems remain poorly understood in terms of the functional interactions that sustain these ecosystems. Research over the past century has focused largely on physiognomic, floristic, and edaphic characterizations, whereas critical biotic processes, such as plant-animal interactions and seed dispersal, have received comparatively little attention. Fragmentation, exotic plantation encroachment, and climate change pose growing threats to these highland systems; however, the mechanisms underlying their natural regeneration remain ambiguous. This thesis

addresses that gap by exploring the seed dispersal ecology and frugivory networks of a keystone Shola tree species, thereby linking biodiversity structure to ecosystem function in a conservation-critical context.

The earliest documentation of Shola forests was concealed in the biographies of many European explorers and hunters who travelled to these regions, as well as in tours and floristic expedition reports. Another excellent source of information on Shola studies are plant explorers and foresters. Previous floras by Bourdillon (1893), Hooker (1872–1897), Gamble and Fischer (1915–1936), and Fyson (1932) also referred to these forests. The first to do a thorough investigation of Shola forests was Ranganathan (1938). He specifically mentioned the physiognomy, species composition, and other factors that influence the existence and distribution of Sholas and grasslands. His hypothesis challenged the prevailing dual climax theory in the Shola-grassland ecosystem, contending that topography affects the distinct climatic climaxes that exist between Shola and grasslands.

This theory contradicts Clement's ecological system and causes disputes among ecologists. Bor (1938) was among the first to challenge the dual climax idea, who contended that Sholas are the remains of an evergreen forest climax that has been driven back by fire and grazing, whereas grasslands are biotic climaxes established by similar forces. Champion (1935, 1936) agreed with this viewpoint stating that clearings had previously taken place and that periodic grazer fires were responsible for the current pattern of grassland. Meher-Homji (1965, 1969, 1986, 1990) studied the ecology of the Palani's Shola grassland and the Nilgiris in detail. He argued that hill stations have a tropical montane climate rather than a temperate climate based on trends in diurnal temperature patterns. He claimed that destroyed Sholas give way to scrub savannas, which eventually degrade further to become grasslands and barren rocks.

Razi carried out earlier research on seed dispersal in Shola in 1950, 1954, and 1955, and these investigations contributed to our understanding of Shola distribution patterns. In the hills of South India, migratory birds "dispersal is the primary cause of Himalayan and Srilankan species," according to Blasco (1970a). He ruled out the possibility that the mountains would remain physically continuous as well as the impact of significant topographic or climatic changes that would have facilitated their migration.

Various opinions have been voiced regarding the regeneration of Shola. According to Bor (1938) and Meher-Homji (1969), most Shola tree species produce drupaceous fruits that yield few seeds that cannot migrate or aggregate. Theagarajan (1971) and Vishnu-Mittre and Gupta (1965) suggested that natural regeneration is inadequate in Shola. Puri et al. (1989) found that Shola species may regenerate under conditions of forest cover, despite their poor regeneration in open regions. The recalcitrance of Shola seeds, which lose viability in a few months, seems to have an impact on germination, according to Kumar and Chacko (1999). Pascal (1988) discussed how frost affects high-altitude grasslands, and proposed that frequent fires and low humidity kill saplings of forest species in savannas. Nair (1994) supported this by pointing out that regular fires alter the local edaphic conditions and encourage the establishment of high-altitude grasslands.

In the Kerala segment of the Western Ghats, Eravikulam National Park has emerged as a key research site. Studies in Eravikulam National Park focused solely on the low-altitude Shola regions surrounding the Rajamala tourist zone (about 1800 m), Jose et al. (1994) examined the structural, floristic, and edaphic features of the Shola-grassland vegetation in Eravikulam National Park. Because Sholas can be found in the Anamudi region at elevations as high as 2680 m, this study could not provide an exhaustive account of the vegetation. During their investigation of the grasslands in Eravikulam, Karunakaran (1997) and Karunakaran et al. (1997) noted specific plant species associations along the Shola-grassland ecotones. In the late 1990s, ecological research on Sholas in the state received impetus when the Forest Department began providing regular financing for biodiversity studies. Many organizations have started working on these initiatives Menon (1997), for example, used remote sensing to map and examine the vegetation of Eravikulam. The dynamics of vegetation in the Western Ghats, as well as the ecological features of Eravikulam and Mannavan Shola, were investigated by Swarupanandan et al. (1998, 2000). Small animal populations in southern Indian forest patches were investigated by Shankar and Sukumar (1999).

Since 2000, the number of publications on Sholas has dramatically increased. The diversity of the topics covered also expanded. Publications from the Kerala Forest Research Institute since its decades of research have aided this increase. Most of these studies have focused on the diversity, distribution, and description of species. Nair and Menon (2001) assessed the population and regeneration status of endemic arborescent flora and Nair and Baburaj (2001) used remote sensing to map biodiversity. Along with

other studies examining soil characteristics, runoff, soil microbiology, and fauna of insects and macroinvertebrates, Chandrasekhara et al. (2001) examined disturbed Shola forests. At the Forestry College of Kerala Agricultural University, Sudhakara (2001) established a computerized herbarium and conducted an inventory of Shola trees; Vidyasagaran and Gopikumar (2001) investigated the phytosociology and litter dynamics of the Shola in the Wayanad area. A book including all previously stated papers and numerous other studies on various topics was published by Nair et al. (2001). Narendran et al. (2001) discovered that Shola forests host high floral species diversity with 67 species recorded in a single 1-ha plot. Menon (2001) studied the characteristics of Shola patches and found that the Shola patch size and number vary between regions. He further classified the Shola forests in Eravikulam National Park into three categories of Shola forest cover compared to grassland cover: low (1–25%), medium (26–50%) and high (> 50%).

Kumar et al. (2002) assessed the effects of rainforest fragmentation on the Western Ghats' herpetofauna and small animals. Nandakumar et al. (2001) characterized the soil from the Sholas of Idukki and Wayanad Districts. Studies on the soil microflora in the Eravikulam National Park were conducted by Sankaran and Balasundaran (2001). Thomas and Sankar (2001) examined the crucial role Shola forests play in sustaining watercourses in the high ranges of Kerala. Even though the Shola forests on different sky islands share plant species (Davidar et al., 2007), Nair and Menon (2001) found that 83.3% of the tree flora are endemic to specific islands in Eravikulam National Park. The high diversity of earthworms (Narendran et al., 2001), centipedes, and spiders (Ramachandran, 2001), high endemism of butterflies (Kunte, 2008), and fish (Ghosh, 2001) in Shola have been recorded in different studies. Davidar et al. (2007) found the predominance of plants of Lauraceae and Symplocaceae in the Shola forest habitats. Numerous writers have examined the therapeutic qualities of shoal species (Arun and Asha, 2008; Mukherjee et al., 2000, 2001). Sankaran (2009) researched one of the sky islands in the Kalakad-Mundanthurai Tiger Reserve, comparing grassland communities at various elevations. The findings indicated higher elevations have fewer species, but more heterogeneity. Diverse populations of large animals are also supported by these high-elevation meadows.

From 2010 onward, the focus shifted toward ecological resilience, fragmentation, and restoration. Farooqui et al. (2010) investigated tropical rainforest vegetation, climate, and sea level changes during the Pleistocene in Kerala, India. Their study provided insights into how the Shola landscape was dominated by C4 grasslands, with forests confined to

more humid valleys or bogs. More studies focusing on Shola ecosystem management and conservation have been conducted since 2010. Arceivala (2012) highlighted the threats faced by the "living fossil" Shola plant community in the upper Nilgiris, emphasizing the vulnerability of these ancient ecosystems. Juyal et al. (2013) examined the vegetation composition, diversity, and structure of tropical montane forests (Shola) in the Palni Hills, with a focus on the impact of disturbances. The impacts of fire on plant diversity in Shola forests were investigated by Saravanan et al. 2014. Bunyan et al. (2014) assessed the tree population and species composition across three forest types, including Shola forests, in the Biligiri Rangaswamy Temple Wildlife Sanctuary in Karnataka. Prasad (2015) used a predictive modeling strategy to investigate the influence of topography on the distribution of tropical montane forest fragments. A list of the vascular flora of the Anamudi Shola National Park in the Idukki district of Kerala was provided by Kumar (2015). Mohandas et al. (2016) reported on the structure and floristic composition of a mid-elevational tropical montane forest. Ecological research on the trees of Karian Shola in Parambikulam Wildlife Sanctuary was carried out by Suraj et al. (2016). Joshi et al. (2018) investigated how past forest management practices impacted the dynamics of the Shola-grassland ecosystem in southern India. He also examined the interaction between grasslands and forests in montane forest-grassland ecosystems, focusing on the function of frost in maintaining a specific ecosystem state (Joshi et al., 2020). Patil (2022) conducted a detailed examination of the community ecology of Shola grasslands, and the significance of Shola forests in the Shola grassland ecosystem is explained in his book. Revathy et al. (2023), documented the diversity of trees in Brahmagiri Wildlife Sanctuary to demonstrate the ecological importance of Shola forests. The invasion of tropical montane forests in Western Ghats by *Cestrum aurantiacum* Lindl. Was studied by DAS et al. (2023) to understand the consequences of this invasion. Schmerbeck et al. (2024) explored the potential of tropical montane forest (Shola) tree species for regeneration in abandoned exotic tree plantations in the Western Ghats of India. Compared to other invasive species, this study discovered that Acacia plantations had the highest density and diversity of regenerated Shola trees. Warriar et al. (2024) used temporal analysis of Shola forest pockets in the Nilgiri Biosphere Reserve (NBR) to determine their suitability for species reintroduction. These investigations collectively underscore the fragile equilibrium that sustains Shola-grassland mosaics.

2.2 | Avian studies in Shola forests

Birds are among the most studied faunal groups in the Shola ecosystem. Khan (1978) conducted a study on the biology of the Black-and-Orange Flycatcher, *Ficedula nigrorufa*, which led to succeeding studies investigating the biology of species like White-bellied Shortwing (*Brachypteryx major*) (Robin et al., 2005, 2006, 2010). Subsequent species-specific studies have focused on threatened endemics, including the Nilgiri Wood Pigeon (*Columba elphinstonii*) (Somasundaram and Vijayan, 2010), Nilgiri Pipit (*Anthus nilghiriensis*) (Vinod, 2005), and Nilgiri Laughingthrush (*Strophocincla cachinnans*) (Zarri et al., 2008). These studies have revealed that such species exhibit narrow habitat preferences tied closely to the floristic structure of Shola forests.

Birds in the Shola ecosystem also play a vital ecological role as frugivores and seed dispersers. For instance, Somasundaram and Vijayan (2010) identified a heavy reliance of the Nilgiri Wood Pigeon on Lauraceae species, highlighting avian dependence on specific plant families. Likewise, Mohandass et al. (2014) demonstrated that bird-mediated dispersal supports liana diversity, contributing to vertical structural complexity and forest regeneration. Sridhar (2005) and Raman (2006) examined the density of many Shola endemic species through systematic sampling. Mudappa and Raman surveyed threatened and endemic birds in the Western Ghats, with data available at www.openecology.in. Amateur and professional bird watchers, particularly from the Kerala Birder organization, have contributed significantly to providing information on the species. The status and distribution information for numerous species in Shola habitats (Praveen and Nameer, 2009) has resulted in the release of a recent book (Sashikumar et al., 2011). Khan (1978), Vijayan (2006) and Zarri et al. (2004) studied the effect of plantations on endemic bird species. Robin et al. 2017 reported that two new genera of songbirds (*Sholicola* and *Montecincla*) endemic to the Shola Sky Islands of the Western Ghats, India, represent ancient radiations driven by climate changes. The avian communities in Shola depend on the floral structures and microclimate that the ecosystem provides for essential resources such as food resources and nesting sites that are vital for their reproduction and survival (Bunyan et al., 2012). Despite these advances, gaps remain in understanding seasonal dynamics, reproductive ecology, and movement patterns of many bird species. A recent study by Newport (2023) on the roosting and breeding behavior of Shola birds provides a foundation for such inquiries. However, more longitudinal studies are needed to assess

how avian communities respond to climate variability, forest degradation, and invasive plant species.

Birds are not only effective bioindicators in Shola systems but also key functional agents in forest regeneration. Their foraging, dispersal, and nesting behaviors are closely linked to forest structure and successional dynamics. Strengthening avian ecological studies, especially under future climate and land-use scenarios, remains essential to understanding and conserving the integrity of the Shola-grassland mosaic.

2.3 | Studies of mammals in Shola forests

Compared to avifaunal research, the study of mammals in the Shola forests of the Western Ghats remains underdeveloped, despite the ecological significance of mammalian guilds in shaping forest dynamics. The most studied animal in the Shola grassland ecosystem is Nilgiri Tahr (*Nilgiritragus hylocrius*), with most studies focusing on natural history observations. The distribution, population status, habitat utilization, and conservation significance are the main subjects of countless research conducted over the last 30 years (Daviadar, 1976; Abraham et al., 2006). Except for the Nilgiri langur (*Semnopithecus johnii*), primates are uncommon in Shola forests, as per the survey conducted by Kumara (2004). Beyond the Nilgiri Tahr, research on other mammalian taxa in Shola ecosystems has been sporadic and taxonomically skewed. Small mammals, particularly rodents, have been the subject of community ecology studies due to their rapid reproductive rates and sensitivity to habitat edges. Shanker and Sukumar (1998, 1999) demonstrated that population structure and spatial synchrony in rodent communities are highly patch dependent, with distinct patterns emerging in isolated Shola fragments. These findings underscore the effects of fragmentation on demographic stability in mammalian populations.

Primate research, while limited, reveals that only a few species, such as the Nilgiri Langur (*Semnopithecus johnii*), consistently utilize Shola habitats. Other primates, including the Lion-tailed Macaque (*Macaca silenus*), show strong avoidance of fragmented or open grassland areas (Kumara & Singh, 2004; Umopathy & Kumar, 2003). This suggests that Shola forests act more as refugia than as core habitats for many primate species, a pattern likely tied to the limited canopy connectivity and reduced foraging diversity.

Trophic interactions and niche differentiation have also been explored in the context of sympatric arboreal mammals. Sushma and Singh (2006) documented resource partitioning

and interspecific interactions among frugivorous and insectivorous species, revealing fine-scale spatial and dietary segregation. These interactions, though infrequently studied, are crucial to understanding energy flow and competition in these vertically structured forests.

Despite their conservation relevance, large carnivores and other keystone mammals (e.g., civets, porcupines, and fruit bats) remain largely unstudied within the Shola-grassland matrix. The functional roles of mammals as seed dispersers, herbivores, and ecosystem engineers remain poorly documented in these ecosystems. This contrasts with parallel research in other tropical montane systems globally, where mammalian contributions to regeneration and succession are better quantified.

Mammalian research in Shola forests has prioritized a few taxa and has yet to fully address ecological roles across trophic levels. Understanding how mammal populations interact with fragmented landscapes, invasive species, and climate change is critical. Future studies integrating camera-trapping, telemetry, and trophic network modeling could significantly enhance our understanding of mammalian ecology in Shola systems.

2.4 | Seed dispersal in Shola forests

Seed dispersal is a fundamental ecological process that governs plant recruitment, spatial distribution, and community composition in forest ecosystems. Despite the Western Ghats being a global biodiversity hotspot with high levels of plant and animal endemism, seed dispersal remains a significantly understudied topic, particularly in tropical montane systems such as Shola forests. The lack of detailed dispersal ecology studies in these forests poses challenges for understanding regeneration, forest dynamics, and long-term resilience.

Zoochory, or animal-mediated seed dispersal, is the predominant dispersal mode for many woody species. Across India, there are records of 2804 plant species being zoochorically dispersed plant species. Key animal dispersers include hornbills, bulbuls, bears, elephants, civets, fruit bats, and macaques, with six threatened species crucial for dispersing at least 86 plant species (Sengupta, 2021). In the Shola context, this network of dispersers plays a pivotal role in maintaining species diversity and facilitating regeneration, particularly in forest fragments where abiotic dispersal is limited.

However, empirical studies quantifying these interactions in the Shola landscape are rare. Frugivore-mediated seed dispersal has been indirectly inferred in species such as

Lophopetalum wightianum, where Sinha and Davidar (1992) demonstrated how wind speed and canopy height affect seed distribution. While this offers insights into anemochory, few parallel studies explore frugivore behavior, gut retention time, seed fate, or dispersal kernels in the Shola context.

Recent reviews by Sengupta (2021, 2022) and Yadav and Phartyal (2023) highlight the urgent need to map seed dispersal networks across India, especially in biodiversity hotspots. Yet, in the Western Ghats, few studies have linked species-specific dispersal behavior to forest structure, habitat fragmentation, or regeneration success.

Another limitation is the lack of integration between plant functional traits and dispersal mechanisms. Traits such as fruit color, size, pulp content, and phenology are known to influence frugivore attraction and dispersal quality, but these have not been systematically studied in Shola trees. This knowledge gap reduces our ability to predict which species are most vulnerable to disperser loss or habitat degradation.

2.5 | Plant-animal interactions and conservation

Plant-animal interactions are foundational to ecosystem structure and function, influencing processes such as pollination, herbivory, seed dispersal, and predation. In tropical montane ecosystems like the Shola forests of the Western Ghats, these interactions are especially critical due to the high degree of endemism and the fragile balance between forest persistence and grassland expansion. Despite this ecological importance, detailed studies on mutualistic plant-animal networks remain limited.

Among the most ecologically significant of these interactions is seed dispersal, which links plant reproductive strategies with animal foraging behavior and movement patterns. In the Shola context, frugivorous birds, mammals, and bats are hypothesized to be key dispersers of fleshy-fruited tree species, many of which are rare or endemic. Yet, the functional roles and effectiveness of these dispersers have not been extensively quantified, leaving a significant gap in our understanding of forest regeneration potential.

A few studies have begun to explore the reproductive ecology and dispersal mechanisms of select Shola tree species. Mohandass and Davidar (2016) documented the flowering and fruiting phenology of woody plants, providing initial data reproductive phenology and seed dispersal in the tropical montane evergreen forest of Nilgiris. Jeevith and Kunhikannan (2019) expanded this work by characterizing reproductive phenology and

seed dispersal in the tropical montane evergreen forest of Nilgiris. These studies suggest a diversity of dispersal strategies, but do not map them to specific animal vectors or seed fates.

More recently, Nimisha and Sreekumar (2024) examined the seed dispersal ecology of *Elaeocarpus munronii*, a near-threatened, zoochorous tree species endemic to the Western Ghats. Their study identified key frugivores, documented seed predation rates, and assessed germination success across microsites, one of the few attempts to integrate field-based animal behavior with plant reproductive success in this region.

At a broader scale, plant- animal interactions form complex ecological networks where redundancy and specialization co-exist. In such networks, a single animal species may disperse seeds from multiple plant taxa, while individual plant species may rely on a narrow set of dispersers. Donatti et al. (2011) and Schleuning et al. (2011) showed that network structure can influence forest resilience, with more specialized systems being more vulnerable to species loss. These insights, drawn from global studies, are highly relevant to the fragmented and invasion-prone Shola landscape.

The conservation implications of plant-animal interaction studies are profound. A disruption in mutualistic networks, whether through the loss of frugivores, changes in forest structure, or climate-driven phenological mismatches can lead to cascading effects on forest composition and regeneration. As such, conservation strategies must go beyond protecting species in isolation and instead consider the integrity of ecological processes that sustain them. In conclusion, plant-animal interactions, particularly those involving seed dispersal, are integral to Shola forest resilience and biodiversity conservation. This thesis builds on this emerging field by contributing empirical evidence of such interactions in a threatened montane landscape, aiming to inform both theoretical ecology and applied conservation planning in the Western Ghats.

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Seed dispersal syndromes in Shola forests of Eravikulam National Park

ABSTRACT

Seed dispersal is a fundamental ecological process that affects forest regeneration and biodiversity, particularly in unique ecosystems such as tropical montane forests. This study investigated the relationship between diaspore morphology, including fruit pulp type, fruit color, fruit size, and seed size, and different seed dispersal mechanisms in the Shola forests of Eravikulam National Park, located in the Western Ghats of southern India. The primary objective of this study was to assess how variations in diaspore traits influence dispersal mechanisms and explore the implications for forest regeneration and conservation. Field observations and experimental studies were conducted over three years, from 2019 to 2022, focusing on 105 tree species across 25 Shola forest patches. Measuring diaspore traits, documenting dispersal events, and identifying dispersers were included in data collection. Statistical methods, including regression analysis and ANOVA, were used to examine correlations between diaspore traits and dispersal mechanisms. This study revealed significant variation in the effects of different diaspore traits on the success of various dispersal mechanisms. For instance, fleshy fruits with bright colors were more effectively dispersed by birds, whereas lightweight seeds showed greater dispersal distances by the wind. These findings underscore the specialized nature of seed dispersal in Shola forests and highlight the role of specific traits in enhancing or limiting the dispersal process. Understanding these dynamics is crucial for developing targeted conservation strategies to support forest regeneration. These insights can guide efforts to enhance seed dispersal by manipulating diaspore traits and protecting the key dispersers. This study contributes to a deeper understanding of seed dispersal in montane forests and provides practical recommendations for managing and conserving Shola ecosystems amid ongoing environmental change. This study offers valuable contributions to the field of plant ecology and conservation biology by emphasizing the importance of diaspore

morphology in shaping seed dispersal processes and informing effective conservation practices.

3.1 | INTRODUCTION

Tropical montane forests (alternatively called tropical montane cloud forests, or cloud forests) are characterized by high levels of endemism brought on by the limited availability of habitat (Bupp et al., 2004). Situated within the headwater catchments of streams that are seasonal and perennial, these forests frequently offer ecosystem services that are often underestimated in their significance to downstream communities. This is primarily attributed to their distinctive capacity to intercept atmospheric moisture in addition to the precipitation directly received. TMF found within the Western Ghats region of southern India are characterized by compact, isolated patches in a landscape predominantly composed of grasslands delineated by natural edges.

Both temperate and tropical species are found in Shola forests. Families Lauraceae, Rubiaceae, Symplocaceae, Myrtaceae, Myrsinaceae, and Oleaceae, dominate the overstory species, whereas dicotyledonous understory species are dominated by Asteraceae, Fabaceae, and Acanthaceae (Swarupanandan et al., 2001, Davidar et al., 2007). Regeneration of arborescent flora in Shola fragments has historically raised concerns (Vishnu-Mittre and Gupta, 1968). Endemism estimates in Shola vary greatly, from 19.5% (Suresh and Sukumar, 1999) to 83.3% (Nair and Menon, 2001).

Sholas are often characterized as living fossils, primarily because of their limited expansion capacity, which is influenced by the prevailing climatic conditions. The interplay between ground frost and morning sun poses a formidable barrier to sapling survival in grasslands. Generally, woody species inhabiting open grasslands exhibit cold resistance (heliophylic) and extend their range to higher altitudes such as the Himalayas and temperate regions. A significant proportion of Shola species originating from tropical stocks cannot withstand low temperatures in open ecosystems, thus leading to their elimination (Khan et al., 1986). Conversely, the temperature within Shola forests remained consistently stable, fostering ample regeneration within these ecosystems.

Shola tree species belonging to the Lauraceae, Myrtaceae, Rubiaceae, and Oleaceae families produce drupaceous fruits that are characterized by recalcitrant seeds (Kumar and Chacko, 1999). These seeds, which have relatively high moisture contents, are susceptible to desiccation and chilling injuries, as highlighted by King and Roberts (1979). As a result,

the viability period of such seeds is limited, varying from a few weeks to a few months, depending on the species, as observed in studies by Chin and Roberts (1980) and Farrant et al., (1988). Over the last decade, Shola-grassland ecosystem mosaics have experienced extensive loss of habitat. As early as 1843, exotic tree plantations were set up in the grasslands to increase firewood availability (Palanna, 1996). Post-independence tree-plantation programs have also received national (federal) budgetary support (Raghupathy and Madhu, 2007). Except for a few areas that are currently protected as sanctuaries, national parks, and reserve forests, the remaining areas have either been cleared of trees or replaced with plantations of various types such as tea, eucalyptus, wattle, silver oak, pine, and lemongrass. Tropical forests face greater annual habitat loss on a global scale than any other tropical forest biome, as reported by FAO in 1993. Sukumar et al. (1995) predict that the dynamic equilibrium between forest and grassland will be impacted by the growing climate change. This disruption is expected to occur through a decrease in frost occurrence and simultaneous reinforcement of the monsoon, favoring the selection of C3 species. One tool that might be useful for preserving and restoring tropical biodiversity is the use of fruit and seed traits to predict dispersal processes, and thus retain forest regeneration.

Seed dispersal is a demographic bridge that connects the end of the reproductive cycle of adult plants to the establishment of their offspring (Jordano and Herrera, 1995; Nathan and Muller-Landau, 2000; Wang and Smith, 2002; Schupp et al., 2010). It is most likely altered by global changes that affect both plant persistence and migration (Corlett, 2009; McConkey et al., 2012; Howe, 2014). The distribution of seeds and vegetation during natural regeneration is determined by seed dispersal, which is influenced both biologically (such as the weight of seeds, the yield, and how far seeds are from the ground) and environmentally (such as the wind environment, topography, and climate), creates a high level of uncertainty (Kim et al., 2022). The Janzen-Connell hypothesis for maintaining species diversity is based on the concept that effective seed dispersal lowers tree mortality that depends on seedling density and distance from the parent tree (Connell, 1971; Janzen, 1970). Therefore, it is useful to understand and identify seed dispersal models so that seed dispersal can be simulated, and its impact on natural regeneration can be assessed. In nature, seeds are dispersed to other sites by biotic and abiotic dispersal mechanisms such as wind, water, and animals (van der Pijl, 1982).

The diaspores of many plant species have developed specialized morphological characteristics that enable them to use biotic and abiotic dispersal strategies (Van der Pijl, 1969; Wenny, 2001), while animals and birds have morphological, physiological, and behavioral adaptations to locate and consume fruits (Fig. 1). For example, diaspores adapted for dispersal by vertebrates ingest attractive colors to their dispersers or thick coats, which prevents consumption by unsuitable frugivores (Janson, 1983; Lomascolo et al., 2008). Van der Pijl (1982) documents broad suites of fruit or seed characters as **dispersal syndromes** reflecting agents most likely to disperse seeds. The morphological structure and traits of seeds make them more likely to be dispersed away from the mother tree (Tiffney, 1984; Hughes et al., 1994; Griz and Machado, 2001).

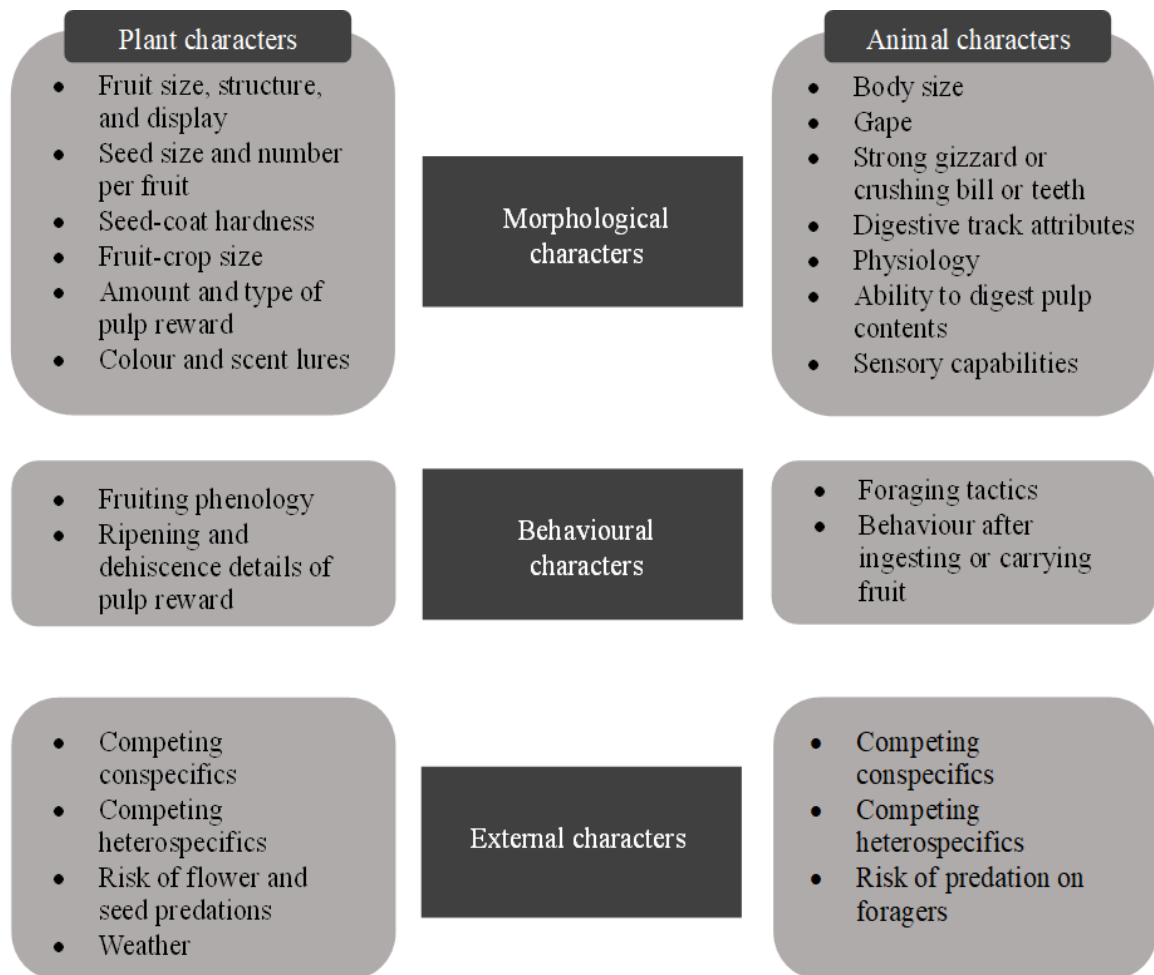


Figure 3.1 Plant and animal characters suitable for seed dispersal

It has been suggested that if seed dispersers are an important evolutionary force, a combination of fruit traits may be used as a basis for predicting potential seed dispersers

(Van der Pijl, 1982; Valenta and Nevo, 2020). Classical dispersal syndromes include anemochory or wind dispersal (the presence of wings or plumes), hydrochory or water dispersal (high buoyancy), myrmecochory or ant dispersal (the presence of elaiosomes), endozoochory (the presence of a fleshy pulp or aril), and epizoochory or external dispersal (the presence of hooks or sticky hairs) (Green et al., 2022). In addition to fruit morphological attributes, chemical composition could also contribute to fruit and seed dispersal syndromes by enabling physiological differences in animal preferences for fruits, as well as frugivore's ability to process macronutrients and metabolize and tolerate toxic compounds (Levey and Martínez del Río, 2001; Karasov and Martínez del Río, 2007; Rojas et al., 2021). Diverse plant habits contribute to the varying degrees of effectiveness of specific dispersal mechanisms, thereby establishing associations between seed dispersal syndromes and plant growth forms. For example, the seeds of tall tree species demonstrate a heightened propensity for wind-mediated dispersal, whereas small vegetation frequently employs ballistic mechanisms for seed dispersal (Thompson and Rabinowitz, 1989; Willson et al., 1990).

The proportion of dispersal modes in a particular vegetation type is defined as the **dispersal spectrum**, which is influenced by community attributes, environmental conditions, and floristic composition (Hughes et al., 1994; Van der Pijl, 1982).

The relative significance of dispersal agents within plant communities can be determined by the study of seed dispersal syndromes (Van der Pijl, 1972; López and Ramírez, 1998). Long-term field observations and other traditional ways of studying ecological processes such as seed dispersal take too much time to offer detailed information on plant-animal interactions. Dispersal syndromes provide a practical concept for the quick and accurate prediction of plant-animal interactions and interdependencies in a community (van der Pijl, 1982; Howe, 1982). In the tropics more often 80–90% of tree species bear fleshy fruits (Howe and Smallwood, 1982; Jordano, 2000; Willson and Traveset, 2000; Osuri et al., 2016). Approximately 65%–90% of woody species in tropical and subtropical Asia are dispersed by vertebrates, with birds being more dispersed than mammals (Datta and Rawat, 2008; Du et al., 2009; Corlett, 2011a; Li et al., 2013; Tadwalkar et al., 2012). However, it is important to note that there is a significant research gap in the study of seed dispersal syndromes, especially in tropical montane forest ecosystems.

Seed dispersal syndromes play a pivotal role in shaping plant community dynamics, biodiversity maintenance, and long-term forest regeneration. In the fragile and fragmented ecosystems of the Shola forests, understanding these syndromes is crucial for predicting plant recruitment patterns and ecological resilience. Due to limited data on plant dispersal in the Shola forests of the Western Ghats, a survey was undertaken on the dispersal modes of tree species in the Shola forests of Eravikulam National Park, located in the southern Western Ghats. The primary objective of this study was to assess the importance of dispersal syndromes and biotic seed dispersal in this forest and to compare these findings with available data from other tropical montane forests.

The main questions addressed in this study are

1. What are the distinguishing diaspore characteristics of the woody species in Shola forests?
2. How do specific fruit and seed traits correlate with the primary seed dispersal mechanisms in Shola forests?
3. What are the conservation implications of the identified seed dispersal syndromes in the management and restoration of Shola forests?

This approach will allow the assignment of dispersal syndromes to tree species in the Eravikulam National Park and also to infer critical plant-animal relationships and interdependencies. In addition, this study aimed to highlight both the unique aspects and similarities of the dispersal syndromes observed in the Shola forest of Eravikulam National Park compared to other tropical forests.

3.2 | METHODS

Study area

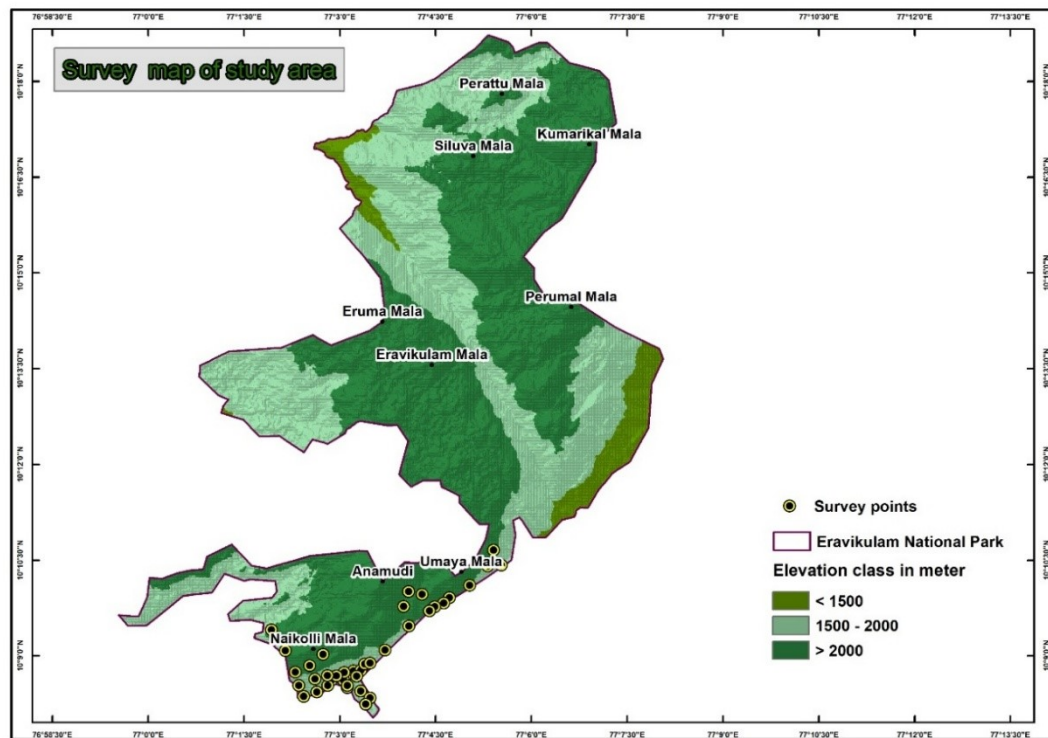


Figure 3.2 Map of the study area (Eravikulam National Park)

Eravikulam National Park (ENP) is located in the Anaimalai Hills (10°05'-10°20'N and 77°0'-77°10'E) in Kerala (Fig. 2). The park (97 km²) consists, of peaks at a maximum elevation of 2695 m surrounding the base plateau that is at an elevation of 2000 m. While the mean maximum temperature recorded in lower elevations varies between 21.9 °C and 22.7 °C, the mean maximum temperature within ENP is as low as 16.6°C. Similarly, the mean minimum temperatures within the ENP were lower than those recorded in the tea estates (13.3 °C). With a mean maximum temperature of 24.1°C, May is the warmest month in ENP, while January is the coldest month with a mean minimum temperature of 3 °C (Rice, 1984). The soil in ENP is classified as Alfisols, described as Arachean igneous in origin, and consists of granites and gneisses (NATMO, 2009). Soils are sandy clay, have moderate depth (30-100 cm) and are acidic (pH 4.1-5.3). The ENP receives approximately 5200 mm of annual rainfall from both the southwest and northeast monsoons, with the southwest monsoon contributing as much as 85% of the annual rainfall. Although contiguous rainforest formations can also be found at lower elevations, the vegetation in

the park is predominantly rolling grasslands interspersed with dense insular Shola fragments.

Dispersal modes of tree species in Eravikulam National Park

Field observations of the dispersal modes of 105 tree species were carried out over three years in 25 different Shola forest patches within the ENP.

All woody stems with a girth at breast height (GBH) of at least 30 cm for this study (considered adult trees in tropical forests) were mapped, measured, identified, and tagged. Species were identified using regional flora. In many cases, common tree species were identified with the assistance of tribal field assistants. Herbarium specimens were collected for further verification by field botanists at Kerala Forest Research Institute, India.

Fruits were collected over three years from 105 fruiting species of canopy and sub-canopy trees between May 2019 and May 2022 from different Shola patches. Fruits were collected based on the following criteria: they were ripe, showed no evidence of parasitism (exit hole or deformed), and had not been aborted (small or deformed) uniformly from each tree. From each tree, fruits meeting these criteria were uniformly collected, with quantities ranging from one to five individuals per species. Subsequently, the collected fruits were carefully placed in sealable plastic bags to mitigate moisture loss and promptly transported to the laboratory for subsequent measurements.

The determination of the seed dispersal mode for tree species was conducted using a multifaceted approach that incorporated various methodologies. These include direct observations of dispersal events, utilization of camera traps to capture dispersal activities, analysis of fruit traits indicative of dispersal mechanisms, examination of animal fecal samples containing seeds, and a thorough review of pertinent literature (Ganesh and Davidar, 2001; Datta and Rawat, 2008). The categorization of tree species into distinct dispersal syndromes was achieved by assigning them to one of five recognized modes of dispersal.

- Ornithochory: Dispersal facilitated by avian species
- Zoochory: Dispersal facilitated by animals
- Anemochory: Dispersal facilitated by wind
- Autochory: Dispersal through mechanical means inherent to the plant itself
- Barochory: Dispersal primarily influenced by gravitational forces

- Hydrochory: Dispersal by water

Our analysis focused solely on the primary phase of dispersal, acknowledging that the seeds of certain species may undergo secondary dispersal by terrestrial rodents.

Fruit characters in Eravikulam National Park

Five fruits from each species were randomly selected for the documentation of various fruit characteristics, including:

- Pulp type: Fruits were categorized as fleshy, dry, fleshy aril, or dry aril.
- Fruit type: The fruits were classified as drupes, berries, capsules, or achenes.
- Fruit color: Diaspore colors were codified according to the following spectrum: black (including dark purple), blue, purple (encompassing greenish purple and purplish brown), brown (including reddish brown), red (including greenish red), green, yellow (inclusive of greenish yellow), orange, grey (including grey-rusty), and white (including greenish white) (Wheelwright and Janson, 1985), which have been widely used in studies of fruit color).
- Fruit size (mm): length and diameter measured using a vernier caliper.
- Seed size (mm): length and diameter measured using a Vernier caliper.

Furthermore, diaspores, whether in the form of fruits or seeds, were classified based on their length and delineated into the following categories: tiny (<2 mm), small (2–5 mm), medium (>5–15 mm), large (>15–40 mm), and extra-large (>40–99 mm) (Duivenvoorden & Cuello, 2012).

The maximum dimensions of the fruits and seeds were used to measure fruit size. We chose the length of the fruit and seed as the measure of size because their dimensions are of more obvious relevance to potential dispersers (Jordano, 1995; Willson et al., 1989) and minimize damage to herbarium specimens. In instances where propagules had appendages such as papery structures, they were integrated into the measurements. Occasionally, the outer layers of the fruits were exceptionally thin, making it impractical to separate them from the seeds. In such cases, fruits and seeds were treated with identical dimensions for measurement.

- Fruit weight: Freshly collected fruits were weighed (0.01 gm using a digital electronic balance).

- Seed weight: Fresh weight measured up to 0.01 gm accuracy using the electronic balance.

Fruits displaying signs of damage were omitted from measurements. These measurements were performed within one day of fruit collection to ensure data integrity. Additionally, a subset of seeds was preserved for use as a reference collection, facilitating comparisons with seeds obtained from the fecal samples.

Efforts were made to collect plant specimens regularly, and these specimens were cross-checked against records in the herbarium of the Department of Forest Botany at Kerala Forest Research Institute, Peechi, India. This rigorous validation process was aimed at ensuring the accuracy and reliability of the collected data.

Data Analysis

Statistical tests and analytical methods were employed to investigate the interrelationships between fruit and seed characteristics and their respective dispersal modes within the Shola ecosystems. Fruit pulp types were classified as fleshy and dry, with frequencies analyzed across bird-, animal-, mechanical-, and wind-dispersed species. The χ^2 test was used to examine the potential correlation between the fruit pulp type and seed dispersal mode. Similarly, fruit types, including berries, drupes, capsules, pods, and achenes, were assessed for their distribution across different dispersal mechanisms and the χ^2 test for independence was used to investigate the association between fruit type and seed dispersal mode. Fruit colors were categorized and χ^2 tests were conducted to explore the relationship between fruit color and dispersal modes. Further analysis involved assessing fruit and seed sizes and employing ANOVA to examine the differences among dispersal mechanisms. Correlation analysis was performed to investigate linear relationships between fruit length, weight, seed length, and seed weight. Finally, Principal Component Analysis (PCA) was applied to reduce the multidimensional dataset, providing insights into the variance in fruit characteristics and dispersal modes.

3.3 | RESULTS

Fruiting trees in Shola forest

A total of 1097 trees were identified, belonging to 105 species and 38 families. The total number of species per Shola patch ranged from 12 to 43. Among the recorded families, the most prevalent were Lauraceae (comprising 20 species), Euphorbaceae (comprising 8

species), and Symplocaceae (comprising 5 species). The distribution of the recorded families throughout the study period is shown in Figure 3.

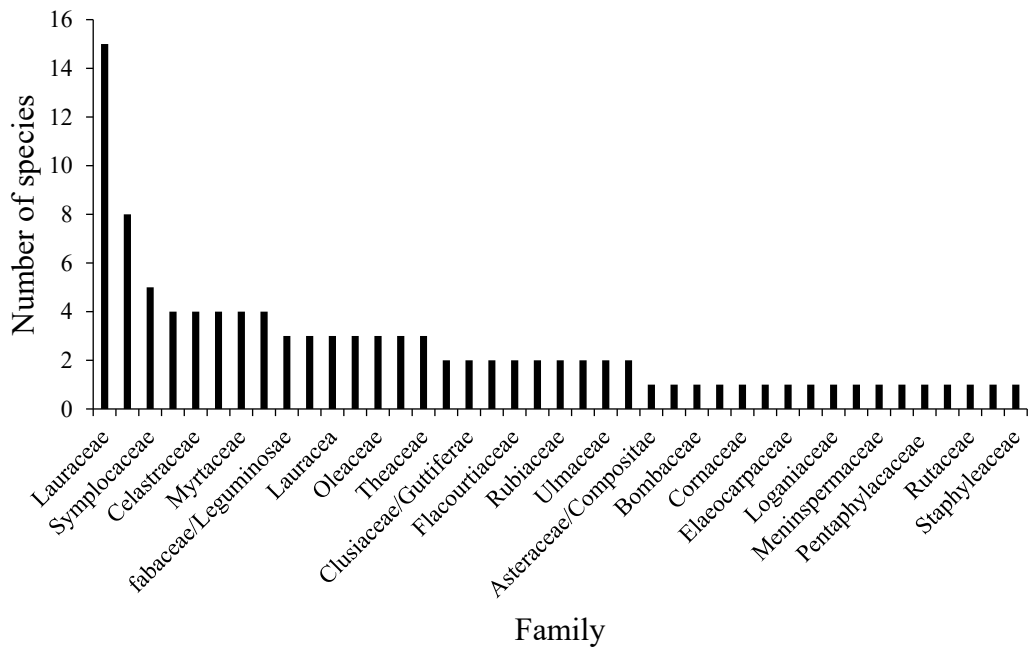


Figure 3.3 Distribution frequency of diverse tree families within Eravikulam National Park

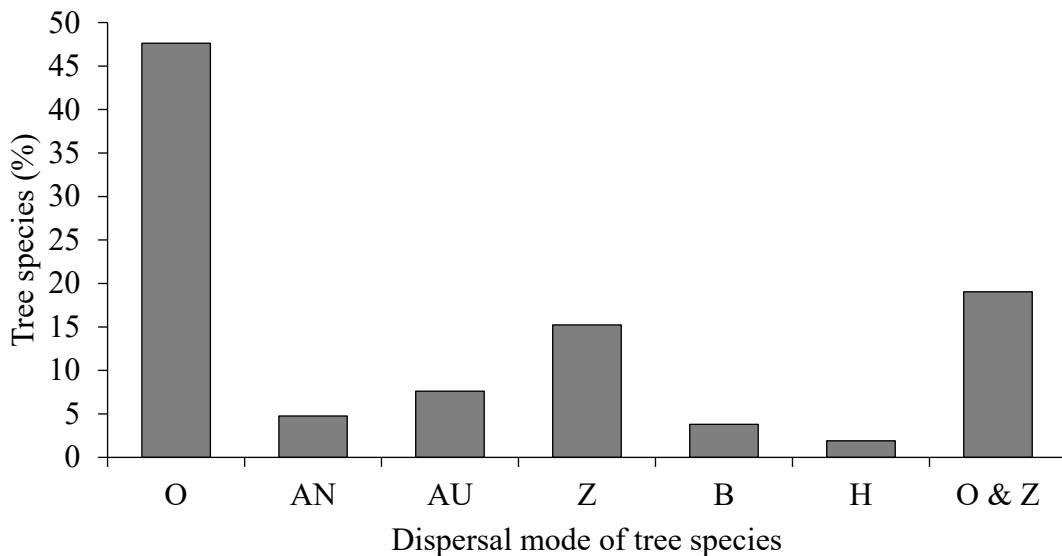


Figure 3.4 Distribution of dispersal modes among trees within the Shola forests of Eravikulam National Park. The percentages represent the proportion of species assigned to each dispersal mode relative to the total number of plant species observed. Ornithochory is denoted by O, zoochory - Z, anemochory - AN, autochory - AU, and barochory - B.

Dispersal syndromes and strategies

Each of the 105 study species was categorized into one of five dispersal syndromes: zoochory, ornithochory, anemochory, autochory, barochory, and hydrochory. Among these, 47.61% were dispersed by avian species, 15.23% by terrestrial animals, and 19.04% by both birds and animals (Fig. 4). Plant families, such as Lauraceae, Symplocaceae, Myrtaceae, and Aquifoliaceae, exhibited a notable prevalence of fruit types suitable for animal dispersal, contributing significantly to the species richness observed in these forests. Conversely, the wind-dispersed species belonged predominantly to families such as Meliaceae, Theaceae, Asteraceae/Compositae, Ericaceae, and Asteraceae/Compositae, each represented by a single genus. Detailed information regarding plant species, fruit and seed characteristics, and dispersal modes is provided in Appendix 1.

Several species, including *Rhododendron arboreum* subsp. *nilagiricum* (Zenker) Tagg, *Magnolia nilagirica* (Zenker) Figlar, and *Elaeocarpus munroi* (Wight) Mast. demonstrated a diverse range of dispersal mechanisms. For each species, diaspore traits, dispersal syndromes, and strategies were assessed and categorized as outlined in Table 1.

Table 3.1 Dispersal syndromes and diaspore characteristics of fruits in ENP, and the distribution of species, genera, and families within each syndrome category.

Dispersal Syndrome	Fruit type of storage material	fruit or seed trait relevant to seed dispersal	Number of species	Number of genera	Number of families
Anemochory	Capsule, Achene, and pod. Winged or hairy or dust seeds for dispersal. Fruits are dry	Easily dispersed by wind	6	6	6
Hydrochory	Light and fibrous	Dispersal through water	2	2	2
Barochory	Capsule, either dry, dry aril or fleshy	Gravitational dispersal of seeds	5	5	5
Autochory	Explosive Capsule, mostly dry.	Explosive dispersal	8	7	5
Zoochory	Endozoochory Berry, drupe (fleshy with high water content, carbohydrate, and fat) or capsule, fleshy or attractive	Edible pulp	37	24	23

Dispersal Syndrome	Fruit type of storage material	fruit or seed trait relevant to seed dispersal	Number of species	Number of genera	Number of families
	Epizoochory Sticky or spiny hooked structure to easily adhere to the animal body	Attached to the animal body for dispersal	3	3	3
Ornithochory	Berry, drupe, or capsule. Mostly fleshy. Seeds are small.	Edible pulp	74	69	38

Bird dispersed species

Of the 105 species in the study area, 50 (47.62 %) were dispersed only by birds (Fig. 2). 23 (21.90%) species showed other dispersal syndromes, along with ornithochory. The important families with fruits dispersed by birds were Lauraceae (20 species), Euphorbiaceae (8 species), and Symplocaceae (5 species). The important genera of Lauraceae found in ENP were *Actinodaphne* (3 species), *Cinnamomum* (3 species), *Litsea* (4 species), *Cryptocarya* (3 species), and *Neolitsea* (3 species). The most common bird-dispersed species were *Ilex* spp., *Cryptocarya* spp., *Neolitsea* spp., *Symplocos* spp. and *Mahonia leschenaultii* (Wall. ex Wight & Arn.) Anon. (Fig. 5).

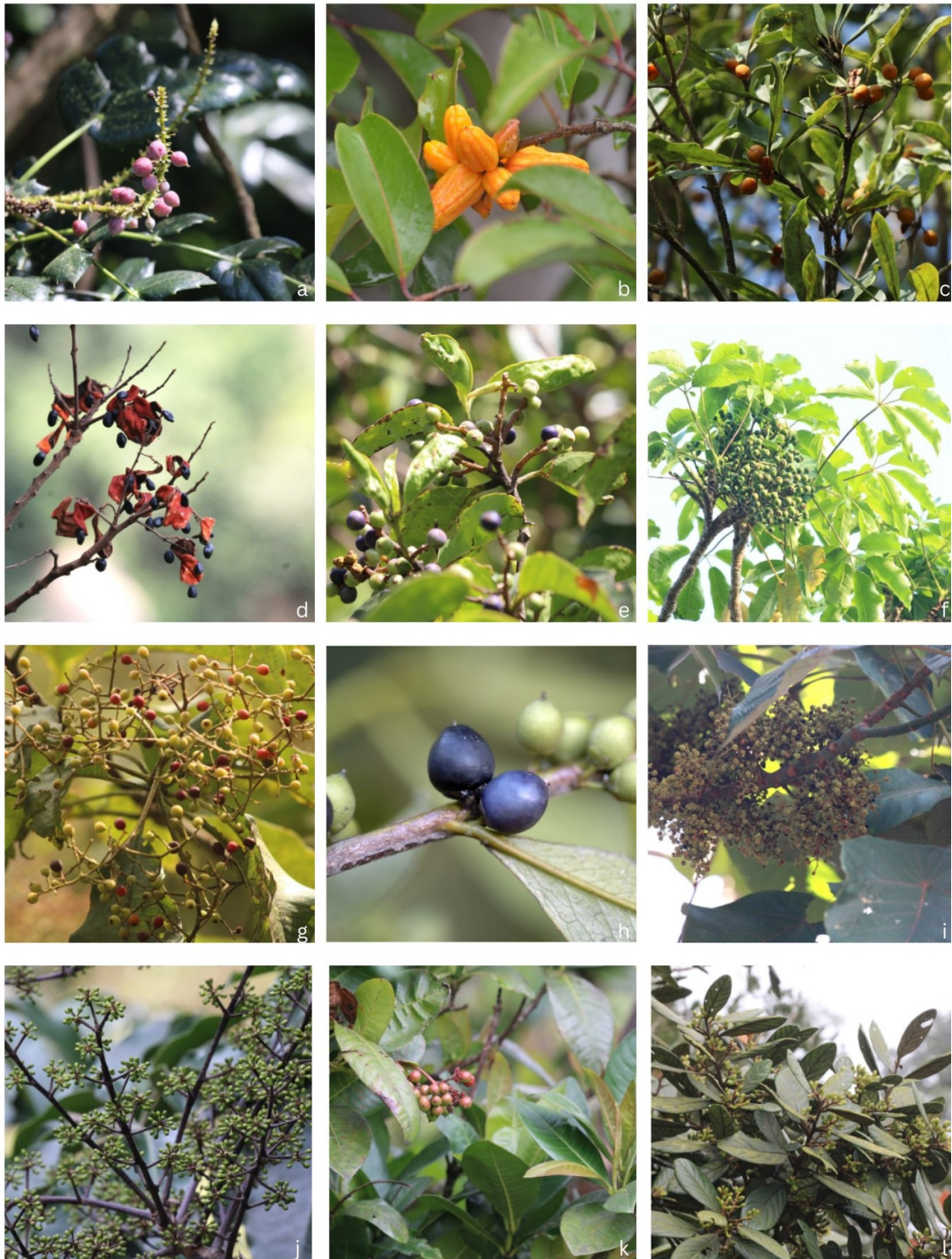


Figure 3.5 Plant species displaying the bird syndrome. a) *Mahonia leschenaultii* (Wall. ex Wight & Arn.) Anon., b) *Casearia thwaitesii* Briq., c) *Pittosporum tetraspermum* Wight & Arn., d) *Abarema subcoriacea* (Thwaites) Kosterm., e) *Symplocos cochinchinensis* (Lour.) S.Moore, f), *Schefflera racemosa* (Wight) Harms, g) *Photinia integrifolia* Lindl., h) *Eurya nitida* Korth., i) *Macaranga peltata* (Roxb) Müll.Arg., j) *Actinodaphne bourdillonii* Gamble, k) *Ixora notoniana* Wall. ex G.Don, l) *Litsea floribunda* (Blume) Gamble.

Animal dispersed species

Of the 105 species studied, the fruits of 40 species were consumed by mammals (Fig. 6). Among these, 16 species (15.23%) were exclusively consumed by mammals, including primates, ungulates, squirrels, civets, porcupines, bears, and elephants, whereas 24 species were consumed by mammals, in addition to other dispersal modes. Among the 16 species solely dispersed by animals, 10 were identified through direct observations and camera traps, whereas the remainder were identified through analysis of scats collected from the study site. Details regarding tree species predominantly consumed by animals and the characteristics of their diaspores are provided in Appendix I.

Prominent plant families associated with animal-dispersed species included Lauraceae (20 species), Euphorbiaceae (eight species), and Symplocaceae (five species). Noteworthy genera frequently dispersed among animals included Symplocos (comprising five species), Litsea (comprising four species), and Ilex (comprising four species), with 17 genera represented by a single species (Fig. 4). Observations have indicated that animals such as the Nilgiri langur (*Semnopithecus johnii*) and the Malabar giant squirrel (*Ratufa indica*) consume fleshy fruits. Additionally, fleshy fruit seeds were found in the feces of the Indian hare (*Lepus nigricollis*) and the brown palm civet (*Paradoxurus jerdoni*).

Bird and animal dispersed species

Twenty-one species (20%) were consumed by both the birds and animals. The important families associated with these species included Aquifoliaceae (4 species), Celastraceae (4 species), Euphorbiaceae (8 species), Meliaceae (4 species), Myrtaceae (4 species), Rosaceae (4 species), and Symplocaceae (5 species). The dominant genera within this category encompassed Actinodaphne (3 species), Cinnamomum (3 species), Cryptocarya (3 species), Elaeocarpus (3 species), Glochidion (3 species), Ilex (4 species), Litsea (4 species), Neolitsea (3 species), Symplocos (5 species), and Syzygium (4 species).



Figure 3.6 Plant species displaying the animal syndrome. a) *Prunus ceylanica* Miq., b), *Mastixia arborea* (Wight) C.B.Clarke, c) *Chionanthus mala-elengi* (Dennst.) P.S.Green, d) *Magnolia nilagirica* (Zenker) Figlar, e) *Fagraea ceilanica* Thunb. f), *Gomphandra coriacea* Wight, g) *Cinnamomum wightii* Meisn., h) *Garcinia cowa* Roxb., i) *Croton malabaricus* Bedd.

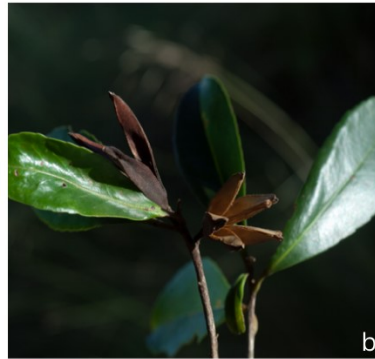


Figure 3.7 Plant species displaying the wind syndrome. a) *Chukrasia tabularis* A.Juss., b) *Gordonia obtusa* Wall., and c) *Dodonaea viscosa* Jacq.

Other dispersal mechanisms in Shola

Additional dispersal mechanisms observed within Shola ecosystems include self-explosions, wind, water, and gravity. Eight species (constituting 7.61% of the total) were identified as undergoing dispersal via self-explosion, originating from six families: Euphorbiaceae, Celastraceae, Thymeleaceae, Magnoliaceae, and Cornaceae. Examples of such species include *Euonymus crenulatus* Wall. ex Wight & Arn., *Microtropis ramiflora* Wight, *Mastixia arborea* (Wight) C.B. Clarke, and *Aporosa fusiformis* Thwaites.

Five species were categorized as wind-dispersed (Fig. 7), four species as gravity-dispersed, and two as water-dispersed. Wind-dispersed species documented in this study were *Vernonia monosis* Benth. ex C.B. Clarke, *Rhododendron arboreum* subsp. *nilagiricum* (Zenker) Tagg, *Pterocarpus marsupium* Roxb., *Chukrasia tabularis* A. Juss., and *Gordonia obtusa* Wall. ex Wight & Arn. (Fig. 5). Fruit dispersed by gravity were *Mesua ferrea* L., *Glochidion ellipticum* Wight, *Fagraea ceilanica* Thunb., and *Aphanamixis polystachya* (Wall.) R. Parker. Species with water as the medium for dispersal included *Rhododendron arboreum* subsp. *nilagiricum* (Zenker) Tagg and *Fagraea ceilanica* Thunb.

Fruit and seed characters

Pulp type

In terms of pulp type, the majority of the fruits (76 of 105, constituting 72.38%) exhibited a fleshy composition, whereas 22 fruits (approximately 20.95%) were categorized as dry. Among the fruits dispersed by avian species, 62 of 73 (84.9%) were fleshy, with a minority (10 of 73, constituting 13.7%) classified as dry. Similarly, a significant proportion of zoochorous fruits (30 out of 40, representing 75%) displayed a fleshy pulp type, whereas 9 out of 40 (22.5%) were identified as dry. Autochorous fruits exhibited a contrasting pattern, with five out of eight species (62.5%) characterized as dry and the remaining three species (37.5%) classified as fleshy. Notably, all species dispersed by wind were characterized as the dry pulp type, as indicated in Figure 8.

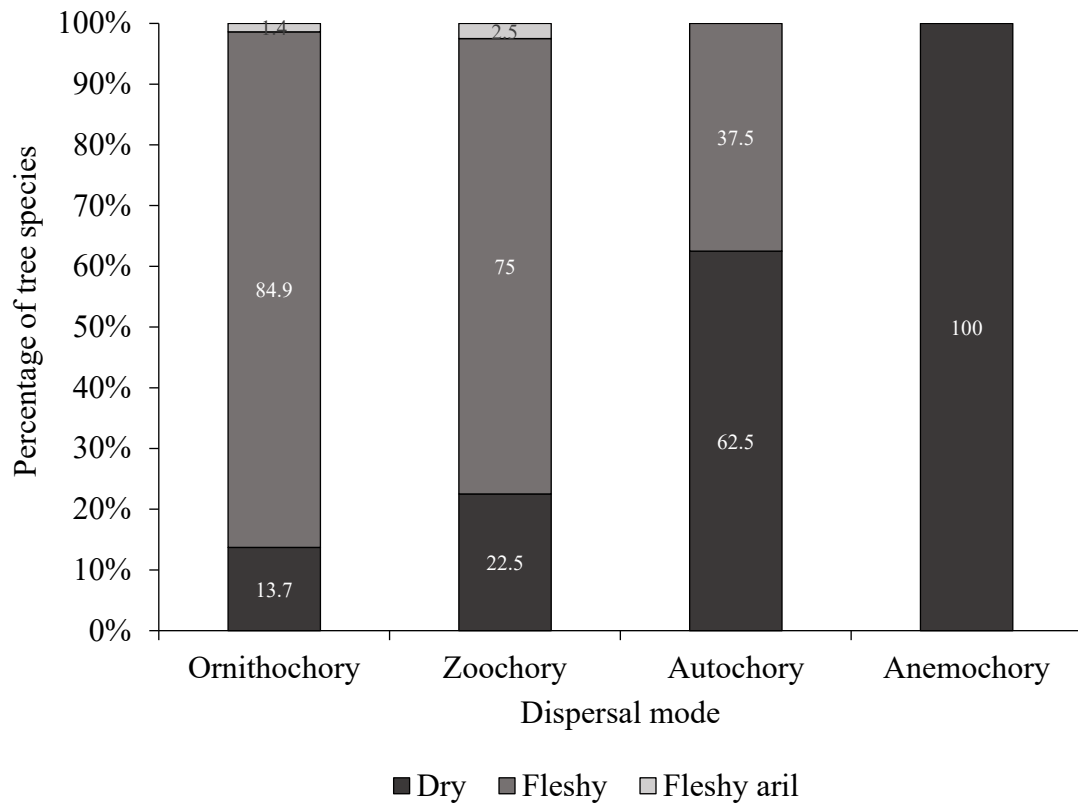


Figure 3.8 Distribution of species based on pulp type

The χ^2 test was used to assess the possible relationship between fruit pulp type and seed dispersal mode within the examined Shola ecosystems. The analysis yielded a statistically significant result, with a computed $\chi^2 = 27.66$ and a corresponding p-value = 0.0001. These findings strongly suggest an association between fruit pulp type and seed dispersal mode within the studied Shola ecosystems.

Fruit type

Birds were predominantly dispersed species, characterized by berries (43.8%) and drupes (41.1%), with capsules (13.7%) and pods (1.4%) exhibiting less frequent avian dispersal (Fig. 9). Notably, ornithochory was not observed in achenes. Animal dispersal was evident in species bearing berries (42.5%), drupes (35%), capsules (20%) and pods (2.5%). The achenes were not dispersed by animals. Autochory primarily occurred in species with capsules (75%), followed by drupes (12.5%), and to a lesser extent, berries (12.5%). Achenes and pods do not rely on autochory for dispersal. Wind dispersal was exclusively observed for achenes (20%) and capsules (60%), and no other pulp type exhibited wind dispersal.

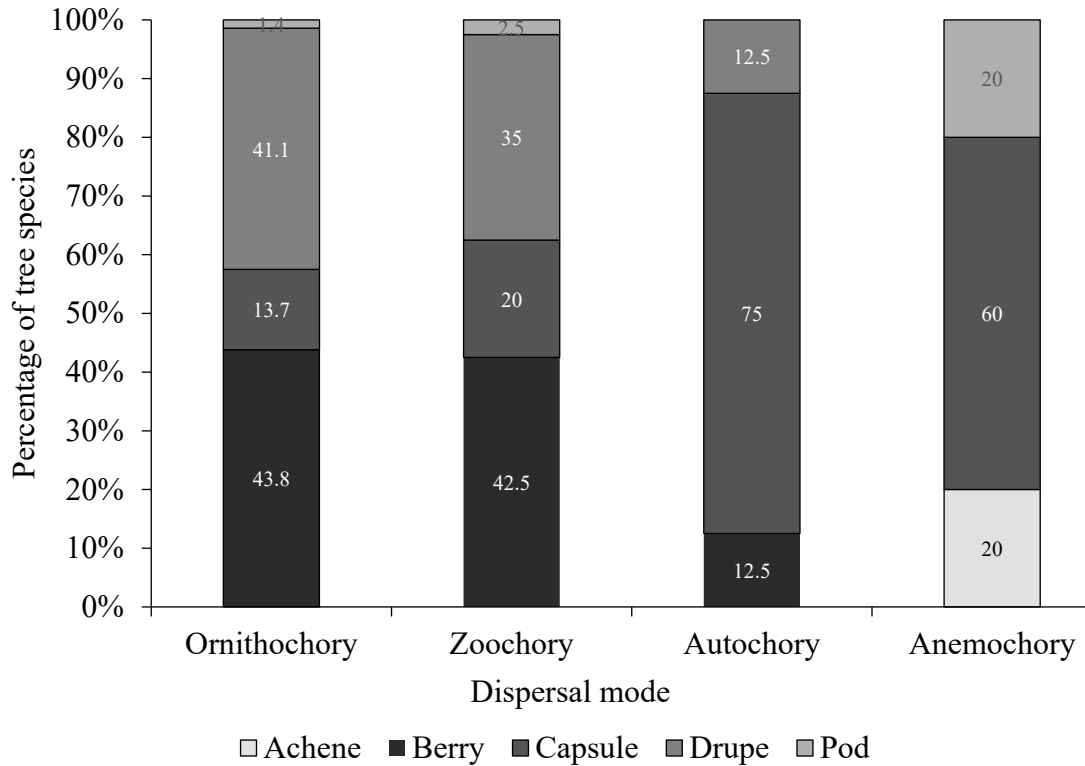


Figure 3.9 Distribution of species based on fruit type and syndromes

The χ^2 test for independence was used to investigate the potential association between fruit type and the seed dispersal mode. The test yielded a statistically significant result ($\chi^2 = 54.95$, $p < 0.00001$), implying a significant association between the fruit pulp type and seed dispersal mode.

Fruit color

Black and purple hues were predominant among the fruits within the Shola forest of the Eravikulam National Park. These colors were most commonly associated with bird-dispersed species, with 26.0% and 23.3% of the species exhibiting black and purple fruit, respectively (Fig. 10). Yellow and brown fruits were moderately represented among the ornithochorous species, comprising 6.8% and 12.3% of the total, respectively.

Brown fruits were most commonly associated with animal dispersal, with 27.5% of the species exhibiting this fruit color. Blue and green fruit exhibited lower frequencies within this category, accounting for 7.5% and 5.0% of the total, respectively.

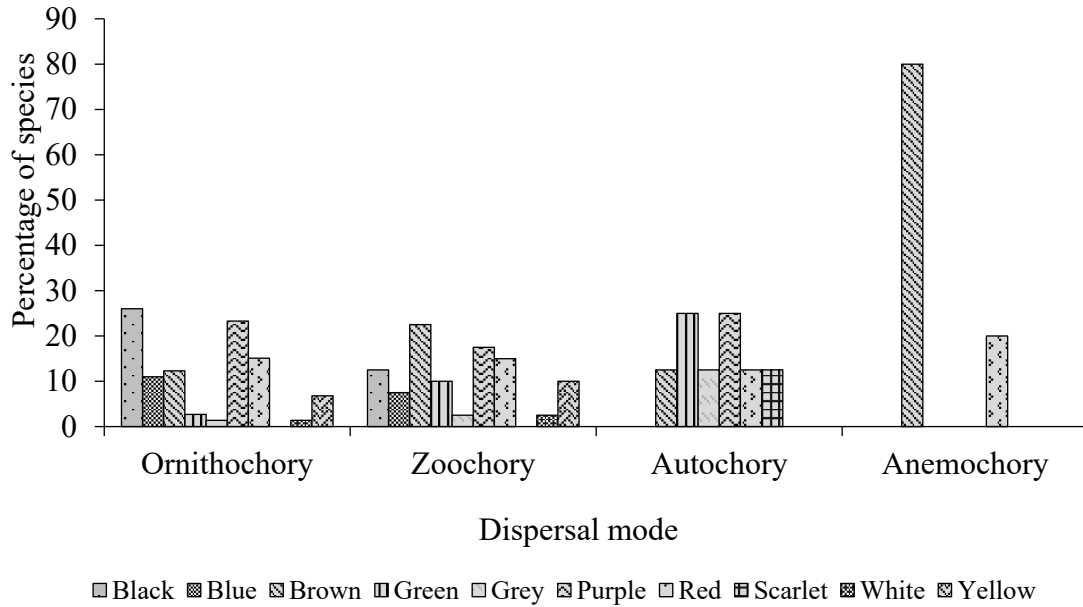


Figure 3.10 Percentage distribution of species based on fruit color

Brown fruits (80%) were dominant among the wind-dispersed species. Brown fruits stand out for their dual association with animal and wind dispersal. In contrast, green and grey fruits demonstrated limited representation within the analyzed dispersal categories.

The χ^2 test was conducted on the association between fruit color and dispersal yielded a significant result ($\chi^2 = 49.33$, $p = 0.0054$). This underscores the non-random relationship between fruit color and dispersal mode, indicating potential ecological relevance.

Fruit and seed size

The length of fruits ranged from 1mm to 50 mm, with notable exceptions being the large fruits of *Chukrasia tabularis* A.Juss. (31.4 mm) and *Fagraea ceilanica* Thunb. (40mm).

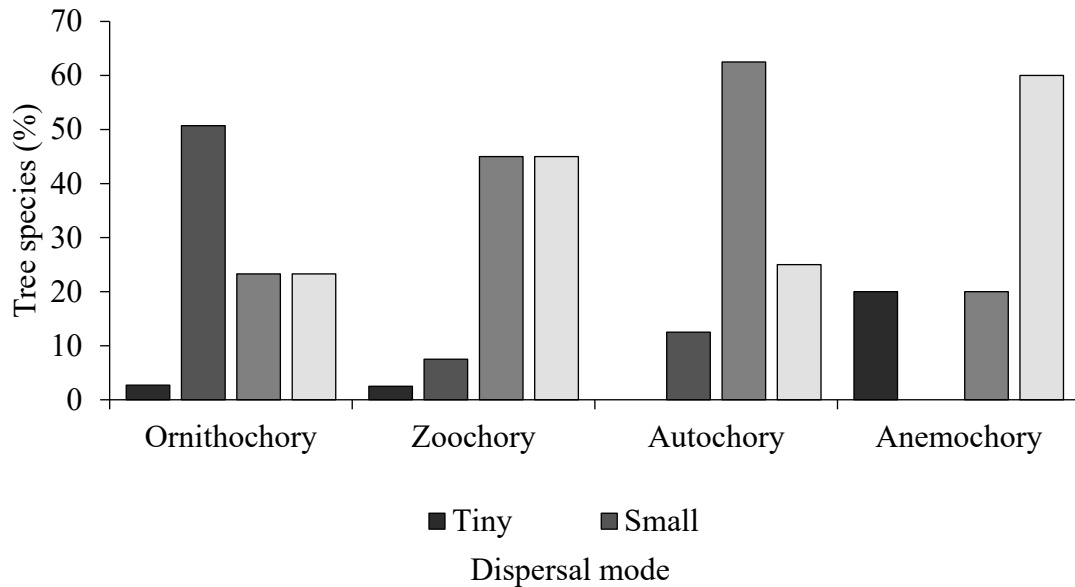


Figure 3.11 Distribution of species based on fruit size (mm). Tiny (<2 mm), Small (2–5 mm), Medium (>5–15 mm), and Large (>15–40 mm).

Small fruits were the predominant category linked to bird dispersal, encompassing 50.7% of the species. In terms of animal dispersal, medium and large fruits were the prevailing categories, accounting for 45% of each of the species (Fig. 11). Medium-sized fruits exhibited the highest representation among autochorous species, with 62.5% relying on self-dispersal. Among the considered fruit sizes, medium-sized fruits were most frequently associated with wind-dispersal mechanisms, comprising 20% of the species.

Anemochorous fruits exhibited the largest mean fruit size (19.10 ± 6.27 mm), significantly surpassing the sizes of fruits associated with other dispersal mechanisms. This difference is attributed to the presence of large-fruited species such as *Chukrasia tabularis* A.Juss., which possess structures conducive to wind dispersal. Zoochorous fruits also displayed a large mean size (16.30 ± 1.99 mm), significantly exceeding the size of ornithochorous fruits (10.45 ± 0.82 mm). The ANOVA results gave an F-value = 4.039, P = 0.009, indicating statistical significance in the fruit size among different dispersal syndromes.

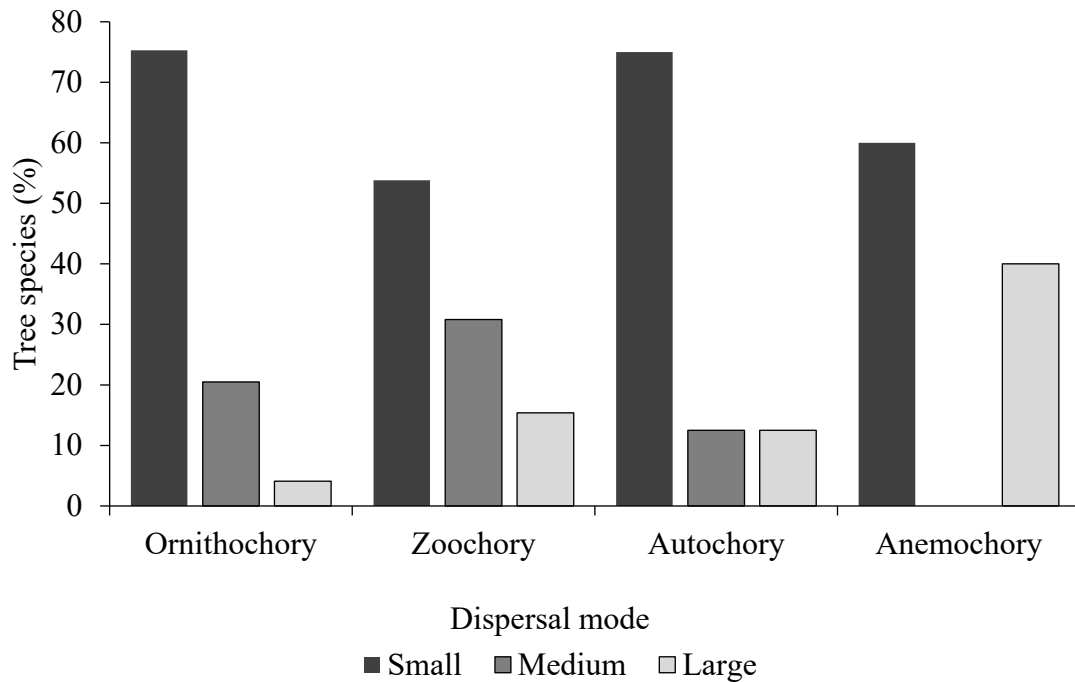


Figure 3.12 Distribution of species based on seed size (mm). Small (2–5 mm), Medium (>5–15 mm), Large (>15–40 mm).

Small-sized seeds were the most prevalent ornithochorous species, accounting for 75.3% (Fig.12). Large seeds have a limited presence in ornithochorous species, with only 4.1% of species exhibiting this seed size. Among the different dispersal syndromes, the proportion of large-sized seeds was higher (6/12) in zoochorous species, although small-sized seeds were dominant in animal-dispersed species, comprising 53.8% of the species. Small-sized seeds were prevalent in all four dispersal categories; large-sized seeds were less common overall and were notably present in animal dispersal (zoochory) and wind dispersal (anemochory).

Autochorous seeds have the largest mean size (18.90 ± 5.92) mm, significantly larger than ornithochorous seeds (10.01 ± 0.90 mm) and anemochorous seeds (12.17 ± 2.41) mm, but not significantly different from zoochorous seeds (10.49 ± 1.24) mm. ANOVA results ($F=2.770$, $p < 0.05$) indicated that there were significant differences in seed size among these dispersal mechanisms.

Fruit and seed weight

The fruit weight ranged from 0.01 g to over 200 g, with the majority of seeds weighing less than 2 g (seed weight range = 0.01 to 15.5 g). Autochorous fruits exhibited the highest

mean fruit weights (4.32 ± 1.83 g), followed closely by zoochorous fruits (4.04 ± 2.18 g), while ornithochorous fruits displayed the lowest mean fruit weight (2.03 ± 0.47 g) (Fig. 13).

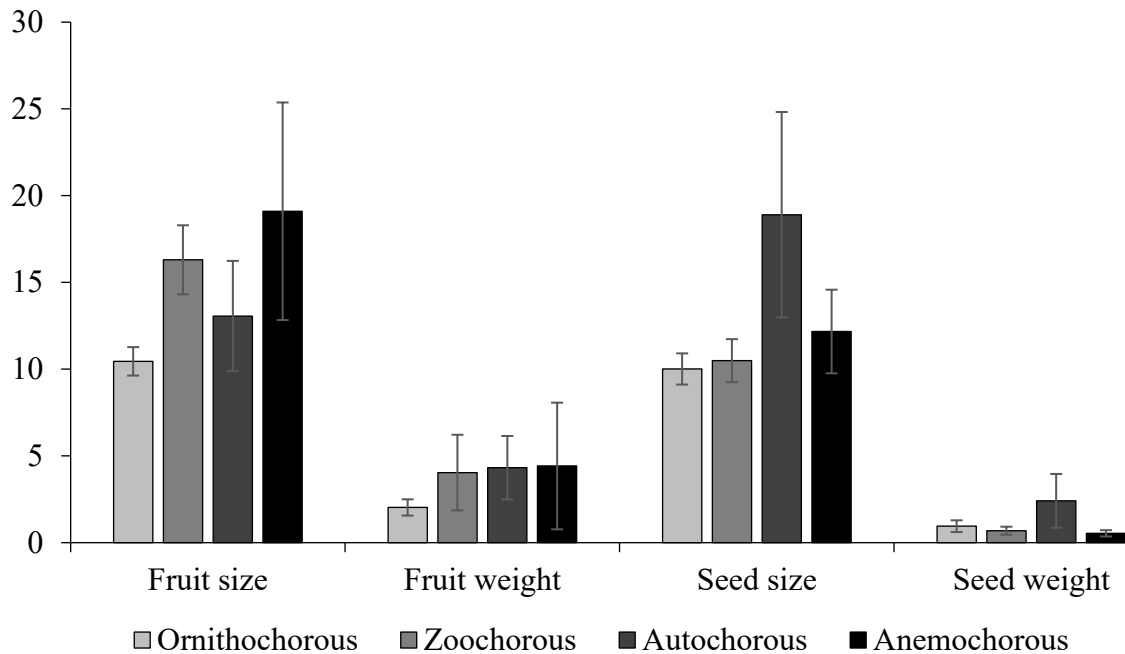


Figure 3.13 Comparison of fruit and seed characters in Shola fruiting species

The ANOVA test for fruit weight (F-value= 0.553, $p = 0.647$) indicated no statistically significant differences in fruit weight among ornithochorous, zoochorous, autochorous, and anemochorous seed dispersal mechanisms. Similarly, the findings also suggested that there were no significant differences in seed weight among the four seed dispersal mechanisms (F= 1.084, $p = 0.360$).

There was no statistically significant linear relationship between fruit length and weight ($r = 0.149$, $p = 0.13$), indicating that changes in fruit length were not consistently associated with changes in fruit weight in a significant manner. Additionally, no strong evidence suggested that changes in fruit length were significantly associated with changes in seed length ($r = -0.074$, $p = 0.454$). Variations in fruit length did not appear to be significantly linked to variations in seed weight ($r = -0.134$, $p = 0.172$). However, a statistically significant positive linear relationship was observed between fruit weight and seed length ($r = 0.226$, $p = 0.020$).

Association between fruit characters

Principal Component Analysis (PCA) of fruit characteristics and dispersal modes effectively reduced the multidimensional dataset into three principal components (PC1, PC2, and PC3), which together accounted for approximately 90.006% of the total variance in the data. PC1 contributed the most, explaining 45.36% of the variance, followed by PC2 (38.11%), and PC3 (16.53%).

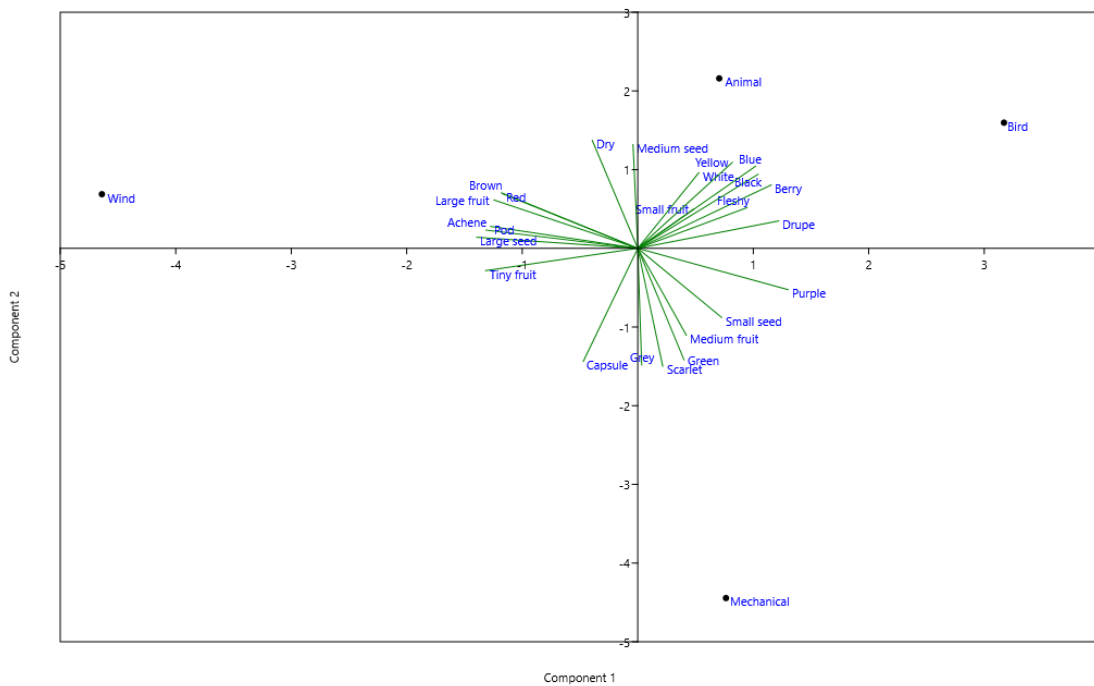


Figure 3.14 Results of the Principal Component Analyses applied to the functional traits of tree species from Shola forests of Eravikulam National Park

Examination of the loadings of dispersal modes on these components revealed that PC1 encompasses a blend of characteristics linked to various dispersal modes, with notably high positive loadings for bird dispersal, and moderate loadings for wind dispersal. PC2 displayed prominent positive loadings for animal dispersal and notable negative loadings for mechanical dispersal. Wind and bird dispersal exhibited moderate PC2 loading. PC3 showed moderate loadings for bird dispersal and relatively low loadings for wind and animal dispersal, with mechanical dispersal displaying negligible loading on this component. Distinct patterns emerged regarding fruit types and colors; fruits characterized by traits such as drupes, berries, fleshy fruits, and small fruit and seed sizes demonstrated

positive loadings on PC1. Similarly, black, blue, and brown exhibited positive loadings for PC1. Medium fruit sizes and specific colors, such as green, grey, and white, displayed positive loadings on PC2, implying an association between these traits and PC2. However, discernible patterns of seed and fruit characteristics strongly associated with PC3 were not evident based on the loadings provided.

3.4 | DISCUSSION

Montane forests harbor a diverse array of woody plant species characterized by various dispersal syndromes and diaspore traits. Our study revealed that the families Lauraceae, Euphorbaceae, and Symplocaceae exhibited significant prominence within the study sites, a trend consistent with prior analyses of neotropical montane forests (Gentry, 1995). Notably, members of the Lauraceae family serve as important dietary components for frugivorous avifauna across regions such as Africa, Southeast Asia, and Australia, as documented in studies by Crome (1975), Snow (1981), and Sun et al. (1997).

The dispersal of fleshy fruits are predominantly associated with vertebrate dispersal mechanisms, a phenomenon well-documented in tropical ecosystems. Muller-Landau and Hardesty (2005) reported that 70%–90% of tropical tree species produce fleshy fruits, which are primarily dispersed by vertebrate frugivores. In Eravikulam National Park (ENP), our study revealed that 48.5% of fruits were dispersed by birds, 14% by animals, and 19% by both animals and birds. These findings align with previous research conducted in tropical forests globally, which consistently demonstrated the prevalence of animal and bird dispersal among woody species (Howe and Smallwood, 1982; Jordano, 1992; Gottsberger and Silberbauer-Gottsberger, 1983; Arbelaez and Parrado-Rosselli, 2005). Our results align with those of Gentry (1982), Howe and Smallwood (1982), Tanner (1982), and Levey and Stiles (1994), who documented a higher proportion of species exhibiting animal or bird dispersal syndromes in montane forest ecosystems. Study results are similar to other studies from Western Ghats, south India (Ganesh and Davidar, 2001; Birand and Pawar, 2004).

Nevertheless, these values are notably lower than those observed in tropical lowland rainforests, where animal dispersal accounts for over 80% of fruit dispersal events (Janson, 1983; Levey and Byrne, 1993). In regions such as New Zealand, which is characterized by temperate forests devoid of large native mammals, fleshy fruits are predominantly dispersed by avian species (Wilson, 1991). The significance of animal-mediated dispersal,

particularly by birds, extends beyond simply moving seeds away from the parent plants. By facilitating seed dispersal, animals, especially birds, enable seeds to evade the heightened mortality risks prevalent near parental trees, where factors such as predation, pathogen abundance, and interspecific competition are most pronounced (Janzen, 1970).

Determining the factors that influence diaspore traits and dispersal spectra of woody plant assemblages in detail is challenging. Willson et al. (1989) suggested that, (1) phylogenetic, geographic, or historic factors; (2) metabolic costs associated with fleshy fruits production; (3) the effectiveness of vertebrate seed dispersal; and (4) constraints resulting from ecological factors unrelated to dispersal might all affect seed dispersal spectra. Historical factors may have a significant influence on the predominance of bird and animal dispersal in the montane forests of the Eravikulam National Park. Given that endozoochory is probably the ancestral dispersal mode of angiosperms, the predominance of avian and mammalian dispersal might simply be a result of the high diversity of flowering plants in these forests (Dilcher, 2000; Feild et al., 2004).

Although the diversity of angiosperm plays a significant role in explaining the predominance of avian and mammalian dispersal in Shola forests, it is not the only contributing factor. Producing fruits and seeds that attract birds and animals is an energetically expensive dispersal strategy for plants. The prevalence of avian and mammalian syndrome in the dispersal spectrum may be influenced by ecological factors, such as the availability of vertebrate dispersers and environmental factors. The high percentage of bird-dispersed fruits can be attributed to the large number of avian dispersers present in the montane forests (Jankowski et al., 2021). More research is required to demonstrate that the dispersal spectra observed in the ENP are connected to the proportion of dispersers and abiotic factors, even though Hughes et al. (1994) claimed that the availability of specific dispersal vectors rarely appears to be an important determinant of dispersal mode.

Wind and ballistic dispersal accounted for 5% and 4% of fruit dispersal within the study area, respectively. Similar low frequencies have been observed in North Queensland (Webb & Tracey, 1981; Irvine & Armstrong, 1990) and Costa Rica (Levey et al., 1994). However, wind dispersal has gained importance in fragmented landscapes like Barro Colorado Island, where it accounts for 16% of large trees (Gentry, 1982). Wind dispersal is more likely to occur in areas with steep topography, such as the study area, or regions

with abundant open forests. Generally, species in wet forests produce a higher proportion of fleshy fruits (Gentry, 1982), whereas species in dry-season deciduous forests are increasingly associated with wind-dispersed taxa (Howe and Smallwood, 1982).

One plausible explanation for the lower occurrence of wind dispersal in ENP Shola forests may be that a substantial distance of seeds must travel to reach open landscapes. Frequent fires and frost can reduce the germination rate of anemochorous seeds in these open areas. This phenomenon highlights the challenges faced by wind-dispersed seeds, which despite being energetically efficient and easy to produce compared to biotic propagules, may have a reduced likelihood of successfully establishing new seedlings because of their limited energy reserves (as discussed by McKey, 1975). Notably, we did not consider the role of fruit bats in the dispersal of seeds in ENP Sholas.

Furthermore, our investigation revealed a notable correlation between the diaspore characteristics and dispersal syndromes within the assessed woody plant species. The predominant traits observed among diaspores associated with ornithochory were the presence of fleshy fruits (such as berries and drupes) exhibiting a black or purple coloration, as well as the presence of small-sized seeds and fruits (ranging from 2-5mm). Conversely, diaspore attributes linked to zoochory encompassed fleshy fruits (including berries and drupes), and medium-to-large-sized fruits typically display a brown coloration. In the present study, autochorous and anemochorous species were comparatively fewer in number. Among these species, diaspore characteristics aligned with autochory include the presence of dry fruits, typically of medium size, exhibiting a green or purple coloration. In contrast, wind-dispersed species, characterized by capsules, predominantly featured dry fruits with brown coloration.

Fleshy fruit was the dominant fruit type observed in the present study. Our data indicate a comparable proportion of functionally fleshy fruits, as found in the rainforests of New South Wales, southern Queensland (Willson et al., 1989), and New Zealand (Clout and Hay, 1989). Ecological and evolutionary studies have highlighted the role of fleshy fruit pulp in promoting seed dispersal, rather than its function in protecting seeds (Andrew, 2000). The dominance of berries and drupes appears to be linked to the number of species in plant families that typically produce simple fruits, such as Lauraceae, Aquifoliaceae, and Symplocaceae, all of which are significant floral components of montane forests (Gentry, 1995; Ulloa and Jorgensen, 1995). Conversely, arillate, dehiscent, and multiple

fruit species were less common in the upper montane sites. This scarcity is likely due to the low water turnover in these areas, which is associated with wet soils, low evapotranspiration rates, and high-humidity environments under cold temperatures (Bruijnzeel, 2001).

In our sample, black/purple and blue fruits predominated, reflecting the fact that these colors are universally favored by birds. Similar results from different floral studies of equatorial Andean montane forests in Australia, Costa Rica, Florida, and Peru (Wheelwright and Janson, 1985; Willson et al., 1989), where black-colored fruits predominate are consistent with the predominance of black-colored fruits from Eravikulam National Park. It has been suggested that the dominance of black and purple fruits to different types of vegetation is related to the visual perception by birds, which are seen as the principal dispersers of seeds in temperate and tropical regions and supported by the high diversity of frugivorous birds found in tropical montane forests (Fleming et al., 1987; Willson et al., 1989). The results of our fruit color analysis align with the Dispersal Syndrome Hypothesis (DSH), which postulates that distinct guilds of dispersers favour different fruit colors and broader sets of traits that correspond to the preferences and perceptual capacities of these seed dispersers (van der Pijl, 1969). According to this hypothesis, fleshy fruits are categorized into a bird-syndrome, characterized by small fruits with bright or contrasting colors such as black, purple and blue, and a mammal-syndrome, characterized by larger fruits with dull colors such as brown, green or yellow, often accompanied by features such as odor or protective husk (Janson, 1983; van der Pijl, 1969). The physiological advantages of black and blue fruits can also account for their dominance in Shola. Dark colors such as black, purple, and blue can absorb more solar radiation, increase the temperature, and accelerate the metabolism and ripening of the fruits (Wheelwright and Janson, 1985). Dark colors may provide a protective property to fruits because of the high concentration of anthocyanins, which inhibit fungal growth in fruit tissues (Schaefer, 2011).

In previous studies on frugivory in various tropical rainforests, including Howe and Smallwood (1982), Herrera (1986), and Wheelwright (1985, 1993), the primary determinants of seed dispersal were fruit and seed size. In the present study, we found strong evidence that fruits with certain colors such as brown, green, yellow, and orange tend to be larger than those with bird dispersal-associated characteristics. Smaller and less expensive seeds are favored for recruitment in high-altitude areas because they can

compete better through efficient broadcast dispersal into gaps and forest edges. This pattern has been observed in various montane forests, as indicated in the findings of Dalling and Hubbell (2002). Larger seeds necessitate larger dispersers, which is why fruits in the tropics are larger than those at higher altitudes, where dispersers are generally smaller. Large fruits may produce less concentrated pigments because of the greater metabolic costs involved, and the remaining green or dull-colored fruits can enhance photosynthesis during fruit development, which may support fruit development and growth (Cipollini and Levey, 1991; Carlson and Harper, 1979). Fruit size, seed size, and seed quantity are crucial attributes that influence frugivore's fruit handling time and likelihood of consumption (Levey, 1987). These factors also affect gut passage rates and the potential dispersal distance from the parent tree (Corlett, 2009). Moreover, large seeds have higher survival rates, leading to the recruitment of large-seeded zoochorous species into larger individuals during the seedling stage (Wendt et al., 2022). Environmental factors such as temperature, altitude, and rainfall can influence fruit and seed characteristics in montane forests. For example, plant species in high-altitude montane forests may produce smaller fruits and seeds as adaptations to challenging environmental conditions (Lomáscolo et al., 2010). Variations in soil fertility and nutrient availability can affect the nutrient content and size of the fruits and seeds (Leishman et al., 2000).

PCA revealed distinct associations between dispersal modes and principal components, indicating that different dispersal mechanisms are characterized by unique combinations of fruit attributes. The analysis highlighted specific patterns in fruit types and colors aligned with the principal components. For instance, fleshy fruits tend to cluster with a particular principal component, whereas certain colors, such as black, blue, and purple, show strong associations with others. These patterns suggest an ecological significance in terms of attracting specific dispersers or adapting to particular environmental conditions. Fruit and seed sizes were linked to principal components, with smaller sizes favoring one component and larger sizes predominantly aligning with another. This further supports our finding that fruit and seed size variations may influence the dispersal mechanisms and ecological strategies adopted by plant species in Shola forest ecosystems.

Seed dispersal syndromes in ENP mirrored patterns from other tropical montane ecosystems. Bird dispersal shaped fruit traits like color and size. These findings enhance our understanding of Shola forest ecology and support conservation planning. Integrating dispersal ecology into restoration planning allows for targeted interventions, such as the

reintroduction of key disperser species, enrichment planting with diaspores suited to current vectors, and corridor design that aligns with natural dispersal pathways. For instance, reintroducing frugivorous birds or mammals can restore dispersal functionality in degraded patches. Selecting tree species with fruit traits favored by available dispersers can improve seedling establishment. Similarly, designing corridors that connect fragmented habitats facilitates movement of both diaspores and dispersers, enhancing gene flow and ecosystem recovery.

Despite substantial data on bird and mammal dispersal, certain dispersal syndromes remain underrepresented in the Western Ghats. Myrmecochory (ant-dispersal), and hydrochory (water dispersal) are seldom documented, presenting critical research gaps. Investigating these overlooked vectors will deepen understanding of ecological resilience and inform comprehensive conservation strategies in montane landscapes.

Shola ecosystem under study had seed dispersal patterns that were comparable to those of the other tropical montane ecosystems. These data underscore the significant role of vertebrate dispersers, particularly birds, in shaping the fruit color, size, and dispersal strategies of these species. These findings contribute to advancing our understanding of the ecological processes governing seed dispersal in montane forests and emphasize the need for further research to explore the interactions between dispersers and plant communities, especially in light of ongoing environmental changes. This information is crucial for informing conservation strategies and ensuring the continued diversity and resilience of these ecosystems.

3.5 | IMPLICATIONS FOR CONSERVATION

Shola forests are ecologically unique and hydrologically significant habitats, occupying only 0.14% of the Earth's total land area (Scatena et al., 2010). These forests are globally recognized for their conservation value because of their high beta diversity and endemism (Hamilton et al., 1995; Bruijnzeel et al., 2010), and many new species have been discovered. However, Shola forests face significant threats from human activities including agricultural expansion, grazing, invasive species, and increased fire frequency (Scatena et al., 2010). Changes in precipitation and temperature and precipitation patterns pose serious threats to montane ecosystems (Foster, 2010; Sukumar et al., 1995). Our study underscores the importance of seed and fruit attributes in predicting seed dispersal mechanisms in Shola forests. Understanding dispersal syndromes is crucial for

conservation planning, as these syndromes can identify dispersal agents associated with specific fruiting trees, estimate distances of seed dispersal, and assess the effectiveness of dispersal events. This knowledge is particularly valuable for predicting the establishment of late-successional trees in early-successional habitats, which is vital for ecosystem recovery and resilience. Insights into the fruit and seed characteristics of this species are essential for conservation and restoration efforts in disturbed habitats. Seed dispersal syndromes offer predictive capabilities regarding the consequences of seed dispersal in altered landscapes, helping to guide conservation strategies. Studies on pollination and seed dispersal are therefore critical for maintaining plant diversity in tropical regions and for meeting the consumption demands of local populations (Resende et al., 2019)

3.6 | CONCLUSION

The study of seed dispersal syndromes in the Shola forests of Eravikulam National Park highlights the complex interplay between diaspore morphology and dispersal mechanisms. This research confirms that diaspore traits, such as fruit pulp type, color, and size, significantly influence the effectiveness of different dispersal methods, ranging from wind and water to animal-mediated dispersal. Key findings demonstrate that animal and bird-dispersed species with fleshy and brightly colored fruits benefit from more efficient seed dispersal, leading to higher rates of seedling establishment. In contrast, wind-dispersed species with smaller lightweight seeds can achieve greater dispersal distances. These insights underscore the importance of diaspore morphology in shaping seed-dispersal dynamics and forest regeneration. The results of this study are important for forest conservation and management. By tailoring conservation strategies to the specific diaspore traits of tree species and protecting key dispersers, we can enhance forest regeneration and ensure the persistence of biodiversity in these unique ecosystems. Furthermore, addressing the identified knowledge gaps and applying these findings to other tropical montane forests will contribute to more effective and informed conservation practices. In conclusion, this study provides a foundational understanding of seed dispersal mechanisms in Shola forests and serves as a basis for future research aimed at preserving ecologically important and biodiverse habitats.

3.7 | RECOMMENDATIONS

1. Given that animal-dispersed species show higher survival rates and seedling establishment, protecting and restoring habitats for key dispersers, such as birds and

mammals, is crucial. Efforts should focus on preserving the ecological niches of these dispersers within Shola forests to ensure effective seed dispersal and forest regeneration.

2. Reforestation and restoration projects should consider the morphological traits of diaspores. Species with traits suited for bird and animal dispersal should be prioritized in reforestation plans to leverage the existing animal disperser networks.

3. Incorporate findings on diaspore morphology and dispersal mechanisms in forest management strategies. By understanding the specific dispersal needs of various species, forest managers can design more effective conservation and restoration programs that account for the natural seed dispersal processes.

4. Given the limited research on seed dispersal syndromes in tropical montane forests, future studies should expand to other regions with similar ecosystems. Comparative studies can provide a broader understanding of how diaspore traits influence dispersal mechanisms across tropical montane forests.

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Appendix 1: Fruit morphology and dispersal modes of woody species in Eravikulam National Park

Species	Family	Fruit type	fruit type (fleshy/dry)	Dispersal syndrome	Fruit color
<i>Ixora wightiana</i> Wall.	Rubiaceae	Berry	fleshy	Bird	Purple
<i>Abarema subcoriacea</i> (Thwaites) Kosterm.	Fabaceae/Legumi nosae	Pod	dry	Bird	Red
<i>Actinodaphne bourdillonii</i> Gamble	Lauracea	Berry	fleshy	Bird	Green
<i>Actinodaphne bourneae</i> Gamble	Lauracea	Berry	fleshy	Bird	Yellow
<i>Actinodaphne salicina</i> Meisn.	Lauracea	Berry	fleshy	Bird	Green
<i>Aglaia apiocarpa</i> (Thwaites) Hiern	Meliaceae	Berry	fleshy aril	Animal, Bird	Red
<i>Agrostistachys indica</i> Dalzell	Euphorbiaceae	Capsule	dry	Bird	Blue
<i>Antidesma montanum</i> Blume	Euphorbiaceae	Drupe	fleshy	Bird	Blue
<i>Aphanamixis polystachya</i> (Wall.) R.Parker	Meliaceae	Capsule	dry	Bird, Gravity	Purple
<i>Apodytes beddomei</i> Mast.	Icacinaceae	Drupe	fleshy	Bird	Scarlet
<i>Apollonias arnottii</i> Nees	Lauracea	Drupe	fleshy	Bird	Black
<i>Aporosa fusiformis</i> Thwaites	Euphorbiaceae	Capsule	fleshy	Mechanical ,Bird	Blue
<i>Ardisia pauciflora</i> B.Heyne ex Wall.	Myrsinaceae	Berry	fleshy	Bird	Yellow
<i>Ardisia rhomboidea</i> Wight	Myrsinaceae	Berry	fleshy	Bird	Grey
<i>Beilschmiedia wightii</i> (Nees) Benth. ex Hook.f.	Lauracea	Berry	fleshy	Bird	Green
<i>Casearia thwaitesii</i> Briq.	Flacourtiaceae	Capsule	fleshy	Bird	Blue
<i>Cassine paniculata</i> (Wight and Arn.) Loobr.-Callen	Celastraceae	Drupe	fleshy	Animal, Bird	Green
<i>Celtis philippensis</i> Blanco	Ulmaceae	Drupe	fleshy	Animal	Red
<i>Celtis tetrandra</i> Roxb.	Ulmaceae	Drupe	fleshy	Animal	Red
<i>Chionanthus mala-elengi</i> (Dennst.) P.S.Green	Oleaceae	Drupe	fleshy	Animal	Black
<i>Chionanthus ramiflorus</i> Roxb.	Oleaceae	Drupe	fleshy	Animal	Green
<i>Chukrasia tabularis</i> A.Juss.	Meliaceae	Capsule	dry	Wind	Brown
<i>Cinnamomum macrocarpum</i> Hook.f.	Lauracea	Berry	fleshy	Bird	Purple

Species	Family	Fruit type	fruit type (fleshy/dry)	Dispersal syndrome	Fruit color
<i>Cinnamomum sulphuratum</i> Nees	Lauraceae	Berry	fleshy	Bird	Yellow
<i>Cinnamomum wightii</i> Lukman.	Lauraceae	Berry	fleshy	Bird	Brown
<i>Cocculus laurifolius</i> DC.	Menispermaceae	Drupe	fleshy	Animal	Black
<i>Cryptocarya beddomei</i> Gamble	Lauraceae	Drupe	fleshy	Bird	Brown
<i>Cryptocarya lawsonii</i> Gamble	Lauraceae	Drupe	fleshy	Bird	Brown
<i>Cryptocarya neilgherrensis</i> Meisn.	Lauraceae	Berry	fleshy	Bird	Yellow
<i>Cullenia ceylanica</i> (Gardner) Wight ex K.Schum.	Bombaceae	Capsule	dry-aril	Gravity	Purple
<i>Daphniphyllum neilgherrense</i> (Wight) K.Rosenthal	Daphniphyllaceae	Drupe	fleshy	Bird, Animal	Red
<i>Dodonaea viscosa</i> Jacq.	Sapindaceae	Capsule	fleshy	Animal	Red
<i>Elaeocarpus munronii</i> (Wight) Mast.	Elaeocarpaceae	Drupe	fleshy	Animal, Bird	Yellow
<i>Elaeocarpus recurvatus</i> Corner	Elaeocarpaceae	Drupe	fleshy	Animal, Bird	Blue
<i>Elaeocarpus tuberculatus</i> Roxb.	Elaeocarpaceae	Drupe	fleshy	Animal	Black
<i>Euonymus crenulatus</i> Wall. ex Wight and Arn.	Celastraceae	Capsule	fleshy	Mechanical	Red
<i>Eurya japonica</i> Thunb.	Theaceae	Berry	fleshy	Bird	Brown
<i>Eurya nitida</i> Korth.	Pentaphylacaceae	Berry	fleshy	Bird	Black
<i>Fagraea ceilanica</i> Thunb.	Loganiaceae	Capsule	fleshy	Gravity, Water	Purple
<i>Garcinia cowa</i> Roxb. ex Choisy	Clusiaceae/Guttiferae	Berry	fleshy	Animal	Purple
<i>Glochidion candolleanum</i> (Wight and Arn.) Chakrab. and M.Gangop.	Euphorbiaceae	Capsule	Dry	Mechanical	Black
<i>Glochidion ellipticum</i> Wight	Euphorbiaceae	Capsule	Dry	Gravity	Black
<i>Glochidion neilgherrense</i> Wight	Euphorbiaceae	Capsule	Dry	Mechanical	Black
<i>Gnidia glauca</i> (Fresen.) Gilg	thymeleaceae	berry	dry	Mechanical	Red
<i>Gomphandra coriacea</i> Wight	Icacinaceae	Drupe	fleshy	Bird	Black
<i>Gordonia obtusa</i> Wall. ex Wight and Arn.	Theaceae	Capsule	dry	Wind	Brown
<i>Hydnocarpus alpinus</i> Wight	Flacourtiaceae	Berry	fleshy	Animal	Green

Species	Family	Fruit type	fruit type (fleshy/dry)	Dispersal syndrome	Fruit color
<i>Ilex denticulata</i> Wall. ex Wight	Aquifoliaceae	Drupe	fleshy	Bird	Purple
<i>Ilex gardneriana</i> Wight	Aquifoliaceae	Berry	fleshy	Bird	Purple
<i>Ilex walkeri</i> Wight and Gardner ex Thwaites	Aquifoliaceae	Drupe	fleshy	Bird	Black
<i>Ilex wightiana</i> Wall. ex Wight	Aquifoliaceae	Drupe	fleshy	Bird	Black
<i>Isonandra perrottetiana</i> A.DC.	Sapotaceae	Berry	fleshy	Animal	Purple
<i>Ixora notoniana</i> Wall. ex G.Don	Rubiaceae	Berry	fleshy	Bird	Red
<i>Litsea bourdillonii</i> Gamble	Lauraceae	Berry	fleshy	Bird	Red
<i>Litsea coriacea</i> (B.Heyne ex Nees) Hook.f.	Lauraceae	Berry	fleshy	Bird, Animal	Red
<i>Litsea floribunda</i> (Blume) Gamble	Lauraceae	Berry	fleshy	Bird, Animal	Purple
<i>Litsea wightiana</i> (Nees) Wall. ex Hook.f.	Lauraceae	Berry	fleshy	Bird, Animal	Black
<i>Macaranga peltata</i> (Roxb.) Müll.Arg.	Euphorbiaceae	Capsule	Dry	Bird, Animal	Black
<i>Magnolia nilagirica</i> (Zenker) Figlar	Magnoliaceae	Capsule	Dry	Animal, Bird, Mechanical	Purple
<i>Mahonia leschenaultii</i> (Wall. ex Wight and Arn.) Anon.	Berberidaceae	Berry	fleshy	Bird	Purple
<i>Mallotus tetraococcus</i> (Roxb.) Kurz	Euphorbiaceae	Capsule	dry	Bird, Animal	Brown
<i>Mastixia arborea</i> (Wight) C.B.Clarke	Cornaceae	Drupe	fleshy	Animal, Mechanical	Red
<i>Melicope lunu-ankenda</i> (Gaertn.) T.G.Hartley	Rutaceae	Capsule	dry	Animal	Brown
<i>Meliosma pinnata</i> (Roxb.) Maxim.	Sabiaceae	Drupe	fleshy	Bird	Purple
<i>Meliosma simplicifolia</i> (Roxb.) Walp.	Sabiaceae	Drupe	fleshy	Bird	brown
<i>Mesua ferrea</i> L.	Clusiaceae/Guttiferae	Capsule	dry	Gravity	Yellow
<i>Microtropis ovalifolia</i> Wight	Celastraceae	Capsule	dry	Bird	Black
<i>Microtropis ramiflora</i> Wight	Celastraceae	Capsule	dry	Animal, Mechanical	Purple
<i>Neolitsea cassia</i> (L.) Kosterm.	Lauraceae	Drupe	fleshy	Bird	Black
<i>Neolitsea fischeri</i> Gamble	Lauraceae	Drupe	fleshy	Bird	Blue
<i>Neolitsea scrobiculata</i> (Meisn.) Gamble	Lauraceae	Drupe	fleshy	Bird	Pink

Species	Family	Fruit type	fruit type (fleshy/dry)	Dispersal syndrome	Fruit color
<i>Nothapodytes nimmoniana</i> (J.Graham) Mabb.	Icacinaceae	Drupe	fleshy	Bird	Black
<i>Olea paniculata</i> R.Br.	Oleaceae	Drupe	fleshy	Bird, Animal	Brown
<i>Palaquium ellipticum</i> (Dalzell) Baill.	Sapotaceae	Berry	fleshy	Animal	Yellow
<i>Palaquium ravii</i> Sasidh. and Vink	Sapotaceae	Berry	fleshy	Animal	Green
<i>Persea macrantha</i> (Nees) Kosterm.	Lauraceae	Berry	fleshy	Bird	White
<i>Phoebe wightii</i> Meisn.	Lauraceae	Drupe	fleshy	Bird	Purple
<i>Photinia integrifolia</i> Lindl.	Rosaceae	Drupe	fleshy	Bird	Purple
<i>Photinia notoniana</i> Wight and Arn.	Rosaceae	Drupe	fleshy	Bird	Red
<i>Pithecellobium subcoriaceum</i> Thwaites	Fabaceae/Legumi nosae	Pod	dry	Animal	Brown
<i>Pittosporum tetraspermum</i> Wight and Arn.	Pittosporaceae	Capsule	dry	Bird	Purple
<i>Polyscias acuminata</i> (Wight) Seem.	Araliaceae	Berry	fleshy	Bird	Red
<i>Prunus ceylanica</i> (Wight) Miq.	Rosaceae	Drupe	fleshy	Animal	Yellow
<i>Pterocarpus marsupium</i> Roxb.	Fabaceae/Legumi nosae	Pod	dry	Wind	Blue
<i>Rapanea capitellata</i> (Wall.) Mez	Rosaceae	Drupe	fleshy	Bird	Black
<i>Rapanea thwaitesii</i> Mez	Myrsinaceae	Berry	fleshy	Bird	Grey
<i>Rhododendron arboreum</i> subsp. <i>nilagiricum</i> (Zenker) Tagg	Ericaceae	Capsule	dry	Wind, Animal, Water	Brown
<i>Schefflera racemosa</i> (Wight) Harms	Araliaceae	Berry	fleshy	Bird	Purple
<i>Symplocos cochinchinensis</i> (Lour.) S.Moore	Symplocaceae	Drupe	fleshy	Bird	Red
<i>Symplocos foliosa</i> Wight	Symplocaceae	Drupe	fleshy	Bird, Animal	Purple
<i>Symplocos obtusa</i> Wall. ex G.Don	Symplocaceae	Drupe	fleshy	Bird	Purple
<i>Symplocos acuminata</i> (Blume) Miq.	Symplocaceae	Drupe	fleshy	Bird	Purple
<i>Symplocos pendula</i> Wight	Symplocaceae	Drupe	fleshy	Bird	Brown
<i>Syzygium densiflorum</i> Wall. ex Wight and Arn.	Myrtaceae	Berry	fleshy	Bird, Animal	Brown
<i>Syzygium gardneri</i> Thwaites	Myrtaceae	Berry	fleshy	Bird, Animal	Blue

Species	Family	Fruit type	fruit type (fleshy/dry)	Dispersal syndrome	Fruit color
<i>Syzygium grande</i> (Wight) Walp.	Myrtaceae	Berry	fleshy	Bird, Animal	Black
<i>Syzygium hemisphericum</i> (Wight) Alston	Myrtaceae	Berry	fleshy	Bird, Animal	Black
<i>Ternstroemia gymnanthera</i> (Wight and Arn.) Bedd.	Pentaphylacaceae	Berry	fleshy	Animal, Bird	Red
<i>Ternstroemia japonica</i> (Thunb.) Thunb.	Theaceae	Berry	dry	Bird, Animal	Red
<i>Trichilia connaroides</i> (Wight and Arn.) Benth.	Meliaceae	Capsule	dry	Animal, Bird	Red
<i>Turpinia cochinchinensis</i> (Lour.) Merr.	Staphyleaceae	Berry	fleshy	Animal, Bird	Purple
<i>Vaccinium leschenaultii</i> var. <i>pubescens</i> S.M.Rajendran, S.C.Agarwal and H.N.Verma	Vacciniaceae	Berry	fleshy	Animal	Brown
<i>Vaccinium neilgherrense</i> Wight	Vacciniaceae	Berry	fleshy	Bird	Red
<i>Vernonia monosis</i> Benth. ex C.B.Clarke	Asteraceae/Comp ositae	achene	dry	Wind	Brown
<i>Viburnum coriaceum</i> Blume	Caprifoliaceae	Drupe	fleshy	Bird	Blue

Interactions between fleshy fruits and frugivores in a tropical montane cloud forest in Western Ghats, India

ABSTRACT

Animals and plants are intricately connected via a complex network that includes pollination, seed dispersal, and herbivory. In this chapter, we examine the role of frugivores in seed dispersal within a tropical montane forest ecosystem (locally known as Sholas), focusing on their dietary preferences, interactions, and contribution to plant community structure. Direct observations, camera traps, and fecal analysis were used to document frugivore behavior, fruit consumption, and seed dispersal patterns. The relative abundance of frugivores was recorded through transect walks, and dietary overlap was assessed using Sorensen's similarity index. A quantitative seed dispersal network was constructed to evaluate species properties including species degree, strength, maximum dependence, and interaction asymmetry. Our findings revealed that 53 bird species from 27 families and 21 animal species from 17 families consumed fruits. The major avian frugivores belong to the Pycnonotidae, Columbidae, Cuculidae, Sturnidae, Turdidae, Leiothrichidae, and Megalaimidae families. Among mammals, the primary frugivores belong to the Cercopithecidae, Sciuridae, Viverridae, and Canidae families. We found a significant dietary overlap among bird species, particularly bulbuls and mynas, and revealed that larger fruits were primarily consumed by mammals, such as langurs. Regression models identified the number of fruit species consumed as a critical predictor of species strength and interaction asymmetry. Frugivores that consumed a greater variety of fruits had a higher degree of species and interaction strength, highlighting their importance in maintaining plant diversity. We did not find any fruit-eating animals solely dependent on a particular plant species. These findings enhance our understanding of plant-frugivore interactions, emphasizing the crucial role of frugivores in seed dispersal and forest regeneration. This knowledge is vital for conservation efforts to protect biodiversity and promote ecosystem resilience. Given the low regeneration capacity of

trees in tropical montane forest ecosystems, particularly in degraded areas, it is crucial to evaluate the frugivore groups present to ensure the natural seed dispersal process.

4.1 | INTRODUCTION

Nature is a vast tapestry of interconnected relationships with which organisms continuously interact and depend on each other for survival. Among the intricate webs of connections, mutualistic interactions are remarkable examples of cooperation and interdependence. Pollination and seed-dispersal mutualism have long been acknowledged as locally species-specific (Stanton, 2003); however, most mutualistic interactions have become more complicated and involve multiple species (Howe, 1984). For various reasons mutualist guilds provide effective model systems for examining the mechanisms underpinning species coexistence (Palmer et al., 2003). A better understanding of how multispecies mutualist assemblages can be maintained depends on determining the relative advantages that various mutualists offer to their hosts (Palmer et al., 2008).

Mutualism, as we have seen, encompasses a wide range of interdependent relationships in nature. One particularly interesting example is the mutualistic interaction between frugivores and fruit-bearing plants. Frugivores and fruit-eating animals play vital roles in seed dispersal, thereby ensuring the survival and expansion of plant populations. As frugivores consume fruits, they inadvertently ingest seeds that later pass through the digestive system. Once excreted, these seeds are deposited at different locations, often far from the parent plant, allowing colonization of new areas (Fig. 1). In this mutually beneficial partnership, frugivores obtain nourishment from the fruit, whereas plants benefit from seed dispersal and have the potential to increase their genetic diversity. Thus, the relationship between frugivores and fruit-bearing plants is another captivating illustration of mutualistic interactions in nature.

The fruit traits themselves play a significant role in determining which animals disperse them (Jordano, 1995; Corlett, 1996). The number of frugivores that can disperse the seed is limited by seed and fruit size (Leighton and Leighton, 1983). In general, large frugivores can handle a wider range of fruit sizes than small frugivores (Noma and Yumoto, 1997).

In the tropics, where frugivores are the major group of vertebrates (Gautier-Hion et al., 1985), there have been few studies examined which frugivores disperse seeds and the extent to which plants and animals depend on one another. Basic knowledge about fruit–frugivore interactions, especially the seed dispersal process in forest ecosystems, is

essential for the conservation of endangered animals and the forest itself (Corlett, 1998; Silva and Tabarelli, 2000). The role of frugivores in dispersing seeds is crucial for the conservation of biodiversity in megadiverse tropical systems such as India. There is enormous pressure on India's biodiversity due to anthropogenic activities (Ceballos et al., 2017), and many plants and animals are currently in danger (Vyas, 2012). The biodiversity of the country may be further threatened by a lack of seed dispersion by frugivores. As hunting increases in disturbed habitats, animal-dispersed species are more likely to become extinct (Bennett and Robinson, 2000). Therefore, plants that produce large fruits and/or seeds may be vulnerable to extinction if they lose their natural dispersers. Therefore, identifying and conserving important seed dispersers is crucial for protecting the species of plants they disperse, which in turn ensures the protection of other taxa that are dependent on these plants.

Understanding plant–frugivore mutualisms is critical to conserving tropical montane forests, as these interactions play a fundamental role in shaping forest structure, influencing regeneration dynamics, and ensuring the long-term persistence of plant communities. In the ecologically unique Shola–grassland mosaics of the Western Ghats, characterized by high species endemism and mounting anthropogenic pressures, such mutualisms acquire heightened importance. While global studies on plant–frugivore networks have advanced significantly, there remains a distinct paucity of research on high-elevation tropical systems such as the Sholas, where biotic communities and environmental conditions diverge notably from those in lowland rainforests. This chapter addresses that critical knowledge gap by documenting patterns of frugivory and plant–animal interactions in Eravikulam National Park, thereby enhancing our understanding of the ecological processes underpinning biodiversity maintenance in fragmented montane landscapes.

Building on insights from the previous chapter, which examined seed dispersal syndromes and associated fruit traits of woody plants, this chapter shifts focus to the frugivores themselves, their identity, foraging behaviors, and effectiveness as dispersal agents. Chapter 3 revealed that vertebrate-mediated dispersal predominates in the study system; here, that insight is expanded upon through a functional and quantitative lens. A weighted plant–frugivore interaction network was constructed to elucidate the structure and specialization of the seed dispersal system, incorporating key metrics such as species degree, interaction strength, maximum dependence, and interaction asymmetry (Donatti et

al., 2011). Moreover, traits influencing frugivore efficacy—such as body mass, dietary fruit composition, and the breadth of consumed plant species—were assessed to understand their role in shaping dispersal outcomes. Finally, the chapter evaluates the contribution of frugivores to forest regeneration by analyzing the diversity and abundance of frugivore-dispersed tree species. Collectively, this research offers a nuanced understanding of frugivore-mediated seed dispersal and its implications for conservation strategies aimed at sustaining the ecological integrity of Shola forests.

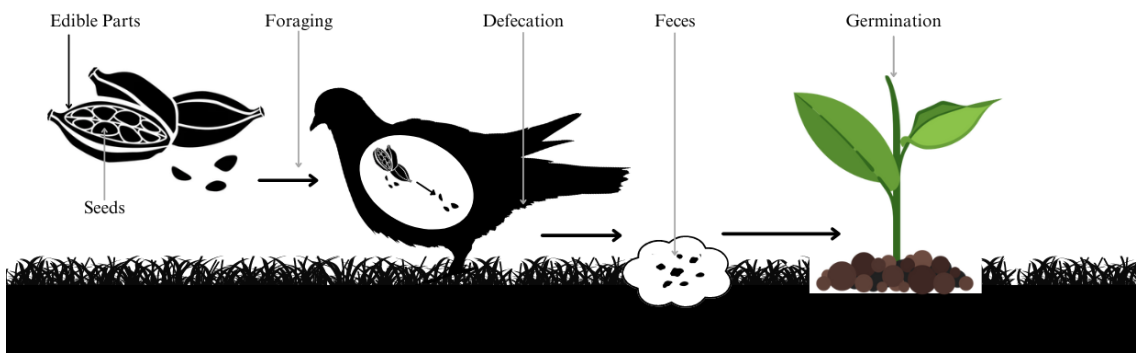


Figure 4.1 Schematic representation of frugivore-mediated seed dispersal and germination

4.2 | METHODS

Frugivore species studied

To gather information about the diets of frugivores, we conducted direct observations, employing an 8-hour diurnal watch from a concealed position approximately 20 m away from the focal tree or animal from 6.00 to 12.00 h and 15.00 to 18.00 h. The trees were observed continuously using binoculars. Focal observations were conducted on the fruiting trees to sample frugivory and seed dispersal by birds and animals. During these observations, we recorded the identity of the bird and/or animal that were distinctly observed, either carrying fruits beyond the canopy or consuming them *in-situ*.

Observations were conducted across three fruiting seasons between May 2019 and May 2022 to capture variation in frugivore activity related to fruit availability. Data collection was distributed across both dry and wet seasons to ensure seasonal representativeness.

Frugivore identification was done visually using binoculars and camera traps and verified using standard field guides. Difficult or ambiguous observations were reviewed independently by two researchers and cross validated with photographs, where available, to ensure observer reliability.

To record the fruit ingestion by mammal species, we strategically placed camera traps beneath fruiting trees. The analysis of fecal samples from various mammalian species has allowed the identification of fruit consumers. For each frugivore visit to the mother tree, we documented pertinent details such as species, average time spent on the tree, number of individuals, item consumed, number of items consumed, and seed processing such as spitting, handling, and swallowing. Using field data, we conducted a comparative analysis of visiting and foraging frequencies among the different disperser species. The gape width of avian frugivores was obtained from previous studies.

Sorensen's similarity index (Krebs, 1989) was used to calculate the dietary overlap between the pairs of frugivores. This index yields a value between 0 and 1, where 0 signifies no overlap and 1 indicates a complete overlap.

Relative abundance of frugivores

A 1 km transect was marked in the primary forest to cover all habitat types. On a fortnightly basis, the transect was walked (at a slow pace of 1 km h⁻¹, noting the mammals seen or observed in the vicinity of the path) between 6.00 -12.00 h and 15.00-18.00 h, preferably during sunny weather. The relative abundance of frugivores was recorded as sightings per kilometer of transect walk. The status of the bird as a frugivore/disperser was determined based on Ali and Ripley (1987) and the direct observations of feeding.

Fruits ingested

Fruits consumed by frugivores were identified by their species name and determined using data from the herbarium collection of the Kerala Forest Research Institute. If unknown, the samples were recorded as non-identified (NID) and collected for later species identification. Fruit species were considered dispersed by endozoochory when the seeds were ingested and defecated intact. Such cases were categorised as frugivory with seed-dispersal mutualism and constituted our list of frugivore-dispersed species. Non-ingested seeds that spat out in an area without primary dispersal were classified as frugivory without endozoochory.

Fruit traits of the frugivore diet

Frugivore fruit samples were collected in the study area between 2019 and 2022. The following fruit characteristics were recorded: fruit type, fruit/seed length, fruit/seed weight, number of seeds per fruit, and fruit color. For species for which fruits were unavailable for collection, we gathered information from the literature.

Seed dispersal/viability/germination/survivorship

Feces were collected from the study site between May 2019 and May 2022. Feces and seeds were weighed (fresh mass), and the number of seeds per fecal sample was counted for each species. For elephant dung, the seed/fruit content of woody plants was counted by hand dissecting and shredding intact dung piles. Germination of seeds and seedlings was also observed. The per cent frequency of occurrence of a given seed type in fecal sample was calculated as

$$\text{Percent Frequency of Occurrence} = \frac{\text{Number of fecal samples containing the seed type}}{\text{Total number of fecal samples observed}} \times 100$$

Germination trials were performed to assess seed viability and the effect of seed passage through the bird/animal gut on germination.

Properties of species in the seed dispersal network

To assess the extent to which frugivore species traits account for the variation in the number and strength of interactions across species in a plant-animal interaction network, we developed a quantitative seed dispersal network that included the number of interactions each animal species had with each fruit species. One seed dispersal event was considered when either:

- i. During focal observations, the fruits were swallowed or removed from the plant species.
- ii. Camera traps detect the removal of fruits from a particular species using a potential seed disperser.
- iii. At least one intact seed of a particular species was found in the scat pile.

Quantitative and qualitative data were used to assess the properties of species in the network. The following properties were recorded (Donatti, 2011):

- a) Species degree: The number of seed dispersal interactions recorded for each plant and animal species.
- b) Species strength- the importance of a species to its partners,
- c) Maximum dependence- dependence of a species on its most important partner
- d) Interaction asymmetry: Relative difference between the interaction strengths exerted by a focal species on the partner species.

All four species properties were calculated for all animal species in the network.

Interaction strength is calculated as

$$\frac{\text{Number of seed dispersal events recorded between two species}}{\text{Sum of the seed dispersal events recorded for the partner}}$$

Value of dependence is calculated as

$$\frac{\text{Number of seed dispersal events recorded between two species}}{\text{Sum of seed dispersal events recorded for the focal species}}$$

Value of maximum dependence of the focal species = Maximum value of dependence calculated for focal species

$$\text{Interaction asymmetry} = \frac{\sum_{j=1}^J (S_{ij} - S_{ji})}{N_i}$$

Where N_i is the degree of species i , S_{ij} is the interaction strength of species i with species j , and S_{ji} is the interaction strength of species j with species i .

For each animal species, we gathered information on the animal body mass, number of fruits consumed, and percentage of fruits in the diet (from the literature), and assessed the density of mammals and bird species. We then tested the associations between these independent variables and the properties of the animal species in the network.

Data analysis

To evaluate the dietary overlap among frugivore groups, Sorensen's similarity index was used to quantify the extent of consumption of shared fruit species across the 12 frugivore categories. A comparative analysis of fruit color preferences, fruit and seed dimensions, and their relationship with frugivore species was performed. Statistical tests, including ANOVA, were used to evaluate variations in fruit length, weight, and seed size among the

different frugivore groups. To explore the properties of species within the frugivore network, correlation analyses were performed to examine the relationships between species density, strength, and number of fruit species consumed. Regression models were constructed to identify the factors influencing species degree, strength, and maximum dependence. The goodness of fit of the regression models was assessed using R-squared values, which indicate the proportion of variance explained by the predictor variables. Durbin-Watson statistics were calculated to evaluate potential autocorrelation within model residuals.

4.3 | RESULTS

Frugivores of Eravikulam National Park

In total, 709 observations of fruit utilization by frugivores were recorded in this study. Seventy-four frugivores from 37 families, including 53 avian and 21 mammalian species, were identified. The avian frugivores were distributed across 45 genera, 27 families, and 6 orders. Among these, 14 species were classified as major frugivores. They were frequently observed and consumed more than 20 fruit species (Appendix 4.1), whereas the remaining species were considered minor frugivores as they were either less commonly observed or consumed fewer than 20 fruit species. The families Muscicapidae (seven species), Columbidae (five species), and Pycnonotidae (five species) were represented by the highest number of frugivorous species, followed by Cuculidae and Turdidae, each with three species. Although many additional bird species have been observed to consume fruits at Eravikulam National Park, these species cannot be considered specialized frugivores because a significant portion of their diet includes insect prey (personal observation). Detailed descriptions of the frugivores are provided below

Avian frugivores in ENP

Bulbuls (Pycnonotidae)

The family Pycnonotidae is represented by five species of bulbuls: grey-headed bulbul (*Brachypodius priocephalus*), red-whiskered bulbul (*Pycnonotus jocosus*), red-vented bulbul (*Pycnonotus cafer*), yellow-browed bulbul (*Iole indica*), and black bulbul (*Hypsipetes leucocephalus*) (Fig. 2). In the Eravikulam National Park (ENP), grey-headed bulbul consumed 20 different fruit species from 13 families, red-vented bulbul consumed 33 species from 14 families, red-whiskered bulbul consumed 48 species from 19 families,

yellow-browed bulbul consumed 16 species from 10 families, and black bulbul consumed 20 species from 13 families. Bulbuls were frequently observed feeding on the fruits of *Macaranga peltata* (Roxb.) Müll.Arg., engaging in both arboreal foraging, where fruits were plucked directly from trees, and aerial foraging, where fruits were captured in mid-air during flight. They repeatedly observed pecking fruits with hard, thick fruit walls, such as *Magnolia nilagirica* (Zenker) Figlar, until the tear allowed access to the pulp. We observed them swallowing the seeds and pulp of smaller fruits and regurgitating the seeds of larger fruits like *Neolitsea cassia* (L.) Kosterm.. In instances where fruit availability was abundant, particularly with *Ilex wightiana* Wall. ex Wight, bulbuls exhibited caching behavior, storing excess fruits in locations such as bark holes for future consumption. Roosting was commonly observed in trees like *Cinnamomum sulphuratum* Nees and *Symplocos cochinchinensis* (Lour.) S. Moore, particularly along the edges of Shola grasslands.



Figure 4.2 Frugivory by Red-whiskered bulbul. Red-whiskered bulbul eating the fruits of A) *Macaranga peltata* (Roxb.) Müll.Arg. (Roxb.) Müll.Arg., B) *Debregeasia longifolia* (Burm.f.) Wedd. (shrub), C) Red-whiskered bulbul on *Symplocos cochinchinensis* (Lour.) S.Moore, D) Fruits of *Photinia integrifolia* Lindl., E) Square-tailed Bulbul feeding the fruits of *Debregeasia longifolia* (Burm.f.) Wedd.

Major fruit sources for bulbuls included *Ilex gardneriana* Wight, *Photinia integrifolia* Lindl., *Macaranga peltata* (Roxb.) Müll.Arg., and *Meliosma pinnata* (Roxb.) Maxim.. The highest feeding activity was recorded on *Symplocos cochinchinensis* (Lour.) S.Moore, *Ilex gardneriana* Wight, *Photinia integrifolia* Lindl., and *Pittosporum tetraspermum* Wight & Arn. during the study period (Table 1).

On average, bulbuls exhibited approximately 3.36 ± 1.70 visitation bouts per hour. Each bout varied in duration, with an average time spent per visitation of approximately 2.63 ± 0.65 minutes. The mean number of fruits consumed per hour by individual bulbuls was approximately 18.36 ± 6.93 .

Table 4.1 Characteristics of frugivory by Bulbuls in their most consumed fruit species

Tree species	Number of visitation bouts by frugivores/hr	Time spent/ visitation bout (min)	Number of fruits consumed by an individual bird/hr
<i>Antidesma montanum</i> Blume	4	3.14	32
<i>Apodytes beddomei</i> Mast.	1	2.59	26
<i>Ardisia pauciflora</i> B.Heyne ex Wall.	2	1.79	14
<i>Cinnamomum sulphuratum</i> Nees	4	3.36	17
<i>Eurya japonica</i> Thunb.	2	2.13	15
<i>Eurya nitida</i> Korth.	3	2.47	28
<i>Ilex gardneriana</i> Wight	6	3.32	16
<i>Ixora notoniana</i> Wall. ex G.Don Wall. ex G.Don	4	2.78	24
<i>Macaranga peltata</i> (Roxb.) Müll.Arg.	3	1.15	7
<i>Meliosma pinnata</i> (Roxb.) Maxim.	2	2.01	12
<i>Neolitsea scrobiculata</i> (Meisn.) Gamble	2	2.33	13
<i>Photinia integrifolia</i> Lindl.	4	3.15	19
<i>Pittosporum tetraspermum</i> Wight & Arn.	5	2.36	19
<i>Symplocos cochinchinensis</i> (Lour.) S.Moore	7	3.15	14

Pearson's correlation test showed a positive correlation ($r = 0.587$, $p = 0.027$) between the time spent by frugivores during visitation bouts and the number of visitation bouts. However, although there was also a positive correlation ($r = 0.494$, $p = 0.073$) between the time spent and fruits consumed, this correlation was not statistically significant at $p < 0.05$. There was no significant linear relationship between the number of visitation bouts and number of fruits consumed.

Doves and Pigeons (Columbidae)

In Eravikulam National Park, the following species were included in this group: the Nilgiri wood pigeon (*Columba elphinstonii*), spotted dove (*Streptopelia chinensis*), emerald dove

(*Chalcophaps indica*), Green imperial pigeon (*Ducula aenea*), and Jerdon's imperial pigeon (*Ducula badia*). The Nilgiri wood pigeon (Fig. 3) was observed to feed on 38 different fruit species from 22 families. The Spotted Dove consumed fruits from 20 species across 15 families, whereas the emerald dove consumed fruits from 12 species from nine families. The green imperial pigeon was recorded to feed on 19 species from 12 families, while Jerdon's imperial pigeon consumed 22 species from 14 families (Table 2). The Lauraceae and Euphorbiaceae families contributed to the highest number of fruit species, with 14 and 15 species, respectively.



Figure 4.3 Roosting of Nilgiri Wood Pigeon (*Columba elphinstonii*) on *Neolitsea fischeri* Gamble.

We consistently recorded the foraging activities of doves and pigeons. They were observed from 06:00 to 18:00 h, with a pronounced foraging peak during the forenoon and a secondary peak in the afternoon. Peak foraging activity occurred between 08:00 and 09:00 in February–May, and between 17:00 and 18:00 in November–January. High visitation rates were recorded for Nilgiri wood pigeons and imperial pigeons on large-seeded tree species, including *Elaeocarpus munroi* (Wight) Mast., *Microtropis ovalifolia* Wight, and

Syzygium densiflorum Wall. ex Wight & Arn., with foraging primarily occurring at the canopy edges. Imperial pigeons spent significantly longer durations on parent trees such as *Aglaia apiocarpa* (Thwaites) Hiern (3.42 ± 0.53 min), suggesting a greater likelihood of seed dispersal occurring beneath the parent tree compared to other Columbidae species. No seed-predating behavior was recorded among the pigeons and doves in this study.

The frugivory patterns observed in pigeons and doves showed that on average, they engaged in 3.7 ± 1.73 visitation bouts per hour for the most consumed fruit species. The average time spent per visitation bout was 2.92 ± 1.49 minutes. The number of fruits consumed by an individual bird per hour was recorded as 43.7 ± 27.48 . (Table 2). Most visitation bouts were recorded on *Daphniphyllum neilgherrense* (Wight) K. Rosenthal (seven visits per hour) and *Syzygium densiflorum* Wall. ex Wight & Arn. (six visits per hour). In Eravikulam National Park, pigeons were observed flying distances exceeding 1 km, although movements could not be tracked beyond this range. Most inter-tree movements were over 300 m, indicating significant travel distances between feeding sites.

Table 4.2 Characteristics of frugivory by pigeons and doves in their most consumed fruit species

Tree species	Number of visitation bouts by frugivores/ hr	Time spent/ visitation bout (min)	Number of fruits consumed by an individual bird/ hr
<i>Ilex wightiana</i> Wall. ex Wight	4	3.04	90
<i>Olea paniculata</i> R.Br.	5	3.79	53
<i>Daphniphyllum neilgherrense</i> (Wight)	7	6.79	4
<i>Cinnamomum sulphuratum</i> Nees	4	3.26	16
<i>Syzygium densiflorum</i> Wall. ex Wight &	6	2.23	15
<i>Neolitsea cassia</i> (L.) Kosterm.	3	1.57	68
<i>Ilex gardneriana</i> Wight	2	1.12	56
<i>Ixora notoniana</i> Wall. ex G.Don	2	2.68	74
<i>Neolitsea scrobiculata</i> (Meisn.) Gamble	2	2.43	22
<i>Symplocos cochinchinensis</i> (Lour.)	2	2.25	39

Pearson's correlation test indicated a positive correlation ($r = 0.730$, $p = 0.017$) between the time spent by pigeons during visitation bouts and the number of bouts per hour. However, the correlations between time spent and the number of fruits consumed ($r = -0.435$, $p = 0.209$), as well as between the number of visitation bouts and the number of fruits consumed ($r = -0.470$, $p = 0.171$), were not statistically significant. We also observed regurgitated seeds of *Neolitsea fischeri* Gamble by pigeons under the parent tree.

Fecal samples of the Nilgiri Wood Pigeon were collected mainly from nesting and feeding sites. The plant parts were often unidentifiable, and identifiable seeds and fleshy portions were documented. Of these 20 fecal samples, five contained only soil particles, 11 contained only seeds, and the remaining plant matter, such as tender shoots, flower buds, and snail shells, while nine species of seeds were identified from the fecal samples. The maximum number of seeds found from the samples were *Ardisia rhomboidea* Wight (31 seeds), *Meliosma pinnata* (Roxb.) Maxim. (27 seeds), *Glochidion ellipticum* Wight (20 seeds), and *Celtis philippensis* Blanco (11 seeds). Species such as *Syzygium grande* (Wight) Walp. (eight seeds), *Pterocarpus marsupium* Roxb. (six seeds), *Mallotus tetraococcus* (Roxb.) Kurz (five seeds), and *Macaranga peltata* (Roxb.) Müll.Arg. (two seeds) were observed to a lesser extent.

Cuckoos (Cuculidae)

In the Eravikulam National Park, fruit consumption has been documented for three species of the family Cuculidae: the Asian koel (*Eudynamis scolopaceus*), Indian cuckoo (*Cuculus micropterus*), and lesser coucal (*Centropus bengalensis*). Among these, the Asian koel is regarded as the most frugivorous species (Fig. 4). The fruits consumed by members of the Cuculidae family in the park included 12 species from 10 families for the Indian Cuckoo, 20 species from 12 families for the lesser coucal, and 30 species from 17 families for the Asian koel.



Figure 4.4 Frugivory by family Cuculidae. Fruits consumed by Cuculidae A) *Nothapodytes nimmoniana* (J.Graham) Mabb., B) *Cinnamomum wightii* Meisn. consumed by cuculidae and C) Asian Koel foraging in Eravikulam National Park

The Asian Koel consistently swallowed whole fruits of *Symplocos pendula* Wight and *Abarema subcoriacea* (Thwaites) Kosterm. or crushing the fruits of *Nothapodytes nimmoniana* (J.Graham) Mabb. before ingestion. The regurgitation of pellets containing seeds was recorded during the observations. On average, cuckoos were found to engage in 3.88 ± 1.13 visitation bouts per hour, with a mean duration of 4.01 ± 1.48 minutes per bout (Table 3). The average number of fruits consumed per hour was 20.63 ± 17.46 , indicating substantial variability in fruit consumption rates. Cuckoos generally consumed whole fruits.

Among the tree species studied, *Syzygium hemisphericum* (Wight) Alston and *Syzygium grande* (Wight) Walp. exhibited the highest number of frugivore visitation bouts per hour, with 3 and 5 visits, respectively. Conversely, *Glochidion ellipticum* Wight recorded the lowest visitation frequency, with frugivores making only three visits per hour. However, during each bout, a relatively large number of fruits (approximately 58) were consumed by individual birds.

Table 4.3 Characteristics of frugivory by Cuckoos in their most consumed fruit species

Tree species	Number of visitation bouts by frugivores / hr	Time spent/ visitation bout (min)	Number of fruits consumed by an individual bird/ hr
<i>Syzygium hemisphericum</i> (Wight)	3	4.07	19
<i>Syzygium grande</i> (Wight) Walp.	5	3.79	7
<i>Cinnamomum wightii</i> Meisn.	6	3.79	6
<i>Daphniphyllum neilgherrense</i> (Wight) K.	4	7.26	11
<i>Syzygium densiflorum</i> Wall. ex Wight & Arn.	4	4.35	15
<i>Glochidion ellipticum</i> Wight	3	2.69	58
<i>Nothapodytes nimmoniana</i> (J.Graham) Mabb.	3	2.34	34
<i>Celtis philippensis</i> Blanco	3	3.78	15

Pearson's correlation analysis of the time spent per visitation bout, number of visitation bouts by frugivores per hour, and number of fruits consumed by an individual bird per hour showed a positive correlation ($r = 0.214$, $p = 0.611$) between the time spent by cuckoos during visitation bouts and the number of visitation bouts per hour. There was a negative correlation ($r = -0.538$, $p = 0.169$) between the time spent by cuckoos during visitation bouts and the number of fruits consumed by an individual bird per hour. A negative correlation ($r = -0.628$, $p = 0.096$) was also observed between the number of visitation bouts of frugivores per hour and the number of fruits consumed by an individual bird per hour. The observed correlations were generally weak or non-significant.

A limitation was encountered during the study that impeded a detailed analysis of the fruits from cuckoo defecation. The insufficient availability of samples restricted the examination

of the dietary content and hindered the identification of specific fruits consumed by these frugivorous birds. The only fruit species identified in the fecal samples were the pulp and seeds of *Syzygium grande* (Wight) Walp. (five seeds), and *Syzygium hemisphericum* (Wight) Alston (two seeds).

Mynas and Black birds (Sturnidae and Turdidae)

Three members of the Turdidae family and one member of the Sturnidae family were observed in ENP. Turdidae family included the pied thrush (*Geokichla wardii*), Nilgiri thrush (*Zoothera neilgherriensis*) Eurasian blackbird (*Turdus merula*), and Sturnidae family included jungle myna (*Acridotheres fuscus*). The major frugivore of the Turdidae family is the Eurasian blackbird, which feeds on the fruits of 27 species (14 families). Most visits by black birds were recorded by *Ardisia pauciflora* B.Heyne ex Wall., *Ilex gardneriana* Wight, *Ilex wightiana* Wall. ex Wight, *Macaranga peltata* (Roxb.) Müll.Arg., *Meliosma simplicifolia* (Roxb.) Walp., and *Photinia integrifolia* Lindl. Other than the fruiting tree species recorded in this study, most sites of Eurasian blackbirds were observed on two shrub species, *Debregeasia longifolia* (Burm.f.) Wedd. and *Maesa indica* (Roxb.) Sweet (Fig. 5).



Figure 4.5 Eurasian blackbird feeding on the fruits of *Debregeasia longifolia* (Burm.f.) Wedd.

Jungle myna has been documented to consume fruits from 32 species across 15 families. Whole-fruit consumption by this species is similar to that of other cuckoo species. Small fruits of *Mahonia leschenaultii* Wall. ex Wight & Arn. were plucked directly from the trees or collected from the ground after falling, thereby initiating pulp extraction. A unique behavior, referred to as "fruit tossing," was recorded when *Photinia integrifolia* Lindl. fruits were consumed, and the fruits were dropped from a height and split upon impact. For larger fruits, such as *Litsea floribunda* (Blume) Gamble, the fruits were held with one foot while being torn apart using the beak. However, smaller fruits were manipulated and opened directly.

Table 4.4 Characteristics of frugivory by mynas and blackbirds in their most consumed fruit species

Frugivore	Tree species	Number of visitation bouts by frugivores / hr	Time spent/ visitation bout (min)	Number of fruits consumed by an individual bird/ hr
<i>Jungle myna</i>	<i>Actinodaphne salicina</i>	7	2.12	12
	<i>Antidesma montanum</i> Blume	6	2.97	41
	<i>Ardisia pauciflora</i> B.Heyne	2	3.01	11
	<i>Eurya nitida</i> Korth.	5	3.26	14
<i>Eurasian Blackbird</i>	<i>Ilex gardneriana</i> Wight	5	3.78	22
	<i>Mahonia leschenaultii</i> (Wall.	3	3.25	31
	<i>Meliosma simplicifolia</i>	5	4.81	14
	<i>Pittosporum tetraspermum</i>	6	5.26	29

The average number of visitation bouts per hour for the jungle myna was found to be 5.0 ± 1.87 , with an average time spent per visitation bout of 2.84 ± 0.43 minutes, and a mean of 19.5 ± 12.46 fruits consumed per hour. In comparison, the Eurasian blackbird exhibited an average of 4.75 ± 1.09 visitation bouts per hour, with a mean time per visitation bout of 4.28 ± 0.80 minutes, and a consumption rate of 24.0 ± 6.67 fruits per hour (Table 4).

Pearson's correlation analysis revealed a positive correlation ($r = 0.042$, $p = 0.921$) between the time spent by these two frugivores during visitation bouts and the number of visitation bouts per hour. A positive correlation ($r = 0.136$, $p = 0.748$) was observed between the time spent on frugivores during visitation bouts and the number of fruits consumed per hour by individual birds. A similar trend was observed ($r = 0.165$, $p = 0.696$) between the number of visitation bouts of frugivores per hour and the number of fruits consumed by the individual birds per hour.

Laughing thrush (Leiothrichidae)

Palani laughingthrush (*Montecincla fairbanki*) was observed feeding on the fruits of 42 species from 20 different families. Larger seeds, such as those of *Magnolia nilagirica* (Zenker) Figlar, were often cracked open using the bird's beak or manipulated against hard surfaces to expose the inner parts for consumption. In contrast, smaller seeds, like those of *Photinia notoniana* Wight & Arn., were swallowed whole, crushed, and ground into smaller fragments before being ingested (Fig. 6).



Figure 4.6 A) Foraging, and B) feeding of fruits by Palani laughing thrush, C) fruits of *Symplocos cochinchinensis* (Lour.) S.Moore, D) Palani laughing thrush feeding on the fruits of shrub *Maesa indica* (Roxb.) Sweet.

The highest number of visits by the Palani laughingthrush was recorded on the shrubs *Debregeasia longifolia* (Burm.f.) Wedd. and *Maesa indica* (Roxb.) Sweet, a pattern similar to that observed in Eurasian blackbirds. Both frugivorous species were found to feed simultaneously on the same tree. Palani laughingthrush was typically observed in groups of 3–15 individuals. These birds were frequently seen at the Shola-grassland edges of Eravikulam National Park, often in the company of bulbuls and mynas.

Table 4.5 Characteristics of frugivory by Palani laughing thrush in their most consumed fruit species

Tree species	Number of visitation bouts by frugivores/ hr	Time spent/ visitation bout(min)	Number of fruits consumed by an individual bird/ hr
<i>Glochidion ellipticum</i> Wight	3	2.14	59
<i>Ilex wightiana</i> Wall. ex Wight	7	3.01	37
<i>Nothapodytes nimmoniana</i>	2	2.75	14
<i>Symplocos foliosa</i> Wight	8	3.11	22
<i>Actinodaphne bourdillonii</i> Gamble	2	1.74	11
<i>Ardisia rhomboidea</i> Wight	3	1.45	37
<i>Prunus ceylanica</i> (Wight) Miq.	4	2.43	22
<i>Celtis philippensis</i> Blanco	2	1.78	9

The average number of visitation bouts per hour for Palani laughing was 3.88 ± 2.20 . The average time spent per visitation bout was 2.30 ± 0.58 minutes, while the average number of fruits consumed by an individual bird per hour was determined to be 26.38 ± 15.89 (Table 5).

Pearson's correlation coefficients between the three variables (time spent per visitation bout, number of visitation bouts of frugivores per hour, and number of fruits consumed by an individual bird per hour) showed a positive correlation ($r = 0.744$, $p = 0.034$) between the time spent by frugivores during visitation bouts and the number of visitation bouts per hour. A positive correlation ($r = 0.017$, $p = 0.968$) was observed between the time spent by frugivores during visitation bouts and the number of fruits consumed by individual birds per hour. There was a positive correlation ($r = -0.0219$, $p = 0.602$) between the number of visitation bouts of frugivores per hour and the number of fruits consumed by

an individual bird per hour. However, there were no statistically significant correlations between variables related to fruit consumption.

Barbets (Megalaimidae)

The small green barbet (*Psilopogon viridis*), a member of the family Megalaimidae, consumed the fruits of 26 species from 17 families within the Eravikulam National Park. During foraging, distinct feeding behaviors were observed in this species (Fig. 7). Typically, barbet perches on branches or tree trunks and scans the surrounding area for ripe fruits. Using its strong bill, the fruits were plucked directly from the branches. Once the fruit was secured, it was held in the bill and the barbet tilted its head backwards to swallow the pulp. Seeds and larger indigestible portions were discarded, which could be a selective feeding strategy focused on maximizing nutrient intake while minimizing waste.



Figure 4.7 Small green barbet found in the Shola forest of Eravikulam National Park

On average, the small green barbet was observed to engage in 3.83 ± 1.33 visitation bouts per hour. The mean duration of each visitation bout was recorded as 3.36 ± 1.05 minutes. In terms of fruit consumption, individual birds consumed an average of 15.33 ± 5.92 fruits per hour (Table 6).

Table 4.6 Characteristics of frugivory by small green barbet in their most consumed fruit species

Tree species	Number of visitation bouts by frugivores/ hr	Time spent/ visitation bout(min)	Number of fruits consumed by an individual bird/ hr
<i>Olea paniculata</i> R.Br.	3	2.14	19
<i>Syzygium hemisphericum</i> (Wight) Alston	5	4.01	17
<i>Gomphandra coriacea</i> Wight	3	3.75	14
<i>Symplocos foliosa</i> Wight	2	2.11	24
<i>Chionanthus ramiflorus</i> Roxb.	5	4.74	10
<i>Cinnamomum macrocarpum</i> Hook.f.	5	3.42	8

A positive correlation was found between the time spent during the visitation bouts and the number of visitation bouts per hour ($r = 0.775$, $p = 0.070$). Negative correlations were observed between the time spent per visitation bout and the number of fruits consumed ($r = -0.724$, $p = 0.104$), as well as between the number of visitation bouts and the number of fruits consumed ($r = 0.779$, $p = 0.068$). Although these correlations indicated strong relationships, the statistical significance was not fully established as the p-values exceeded the typical threshold for significance.

Other frugivorous bird of ENP

The other frugivorous bird community observed in Eravikulam National Park represents a diverse range of avian families, including Picidae, Dicaeidae, Irenidae, Nectarinidae, Sylviidae, and Turdidae. Among the frugivores, the Indian lorikeet (*Trichoglossus chlorolepidotus*) and the Asian fairy-bluebird (*Irena puella*) were notable for consuming the fruits of *Elaeocarpus munroii* (Wight) Mast., *Symplocos spicata* Roxb., *Celtis tetrandra* Roxb., and *Symplocos foliosa* Wight. A Black-hooded Oriole (*Oriolus xanthornus*) was primarily observed feeding on the fruits of *Symplocos pendula* Wight.

Other bird species, such as the bar-winged flycatcher-shrike (*Hemipus picatus*) and fork-tailed drongo (*Dicrurus adsimilis*), were involved in fruit consumption, indicating their role in the frugivory dynamics of the forest. The Nilgiri flycatcher (*Eumyias albicaudatus*) primarily targeted small, manageable fleshy fruits, including *Pittosporum tetraspermum* Wight & Arn. and *Maesa indica* (Roxb.) Sweet. The ashy drongo (*Dicrurus leucophaeus*) exhibited selective feeding behavior, favoring the fruits of *Ixora notoniana* Wall. ex G.Don and *Syzygium hemisphericum* (Wight) Alston. The common iora (*Aegithina tiphia*) displayed a broader diet, consuming fruits from a range of species such as *Isonandra perottetiana* A.DC., *Ziziphus xylopyrus* (Retz.) Willd., *Ixora notoniana* Wall. ex G.Don, and *Ilex wightiana* Wall. ex Wight.

Mammalian frugivores in ENP

Major fruit-eating animals in the ENP include Nilgiri langurs, lion-tailed macaques, Malabar giant squirrels, civets, and jackals.

Langurs and Macaques (Cercopithecidae)

The family Cercopithecidae, which includes primates such as the Nilgiri langur (*Semnopithecus johnii*) and lion-tailed macaques (*Macaca silenus*), exhibits fruit interaction behavior. Feeding activity was observed in selected langur groups (n = 5) at Erachippara, Rajamala, Eighth Mile, and Vaguara. Nilgiri langurs were observed to feed on fruits of 37 species belonging to 23 families. Among these 37 species, langurs were observed feeding on mature fruits of 21 species (Table 7). The remaining fruits were immature. Immature fruits fed by langurs include *Meliosma simplicifolia* (Roxb.) Walp., *Casearia thwaitesii* Briq., and *Cinnamomum sulphuratum* Nees. Nilgiri langurs exhibited various seed-handling techniques, such as spitting (SP) seeds, swallowing (SW) seeds, and pulp. Species such as *Elaeocarpus munroi* (Wight) Mast. and *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. seeds either spat out or pass intact through their digestive tract. In contrast, some species, such as *Cinnamomum macrocarpum* Hook.f., are more likely to be subjected to seed predation (SP), in which seeds are likely to be consumed and destroyed (Fig. 8).

During all observations, the feeding behavioral sequences of the langurs were observed to be of a longer duration, with more feeding acts between 10:00 and 14:00 h. Conversely, shorter sequences were recorded between 14:00 and 18:00 h, as well as between 6:00 and 10:00 h.

The average number of visitation bouts by Nilgiri langur per hour was recorded as 0.40 ± 0.05 . The time spent per visitation bout was measured at 17.93 ± 12.08 minutes, while the number of fruits consumed by an individual per hour was observed to be $38. \pm 3$. Longer feeding times, particularly for species such as *Litsea floribunda* (Blume) Gamble and *Syzygium densiflorum* Wall. ex Wight & Arn., could indicate higher fruit availability or preference for these species.



Figure 4.8 Nilgiri langur from Eighth mile, Eravikulam National Park

Table 4.7 Fruits consumed by Nilgiri langur in ENP

Species	Seed handling	Number of visitation bouts by frugivores / hr	Time spent/ visitation bout (min)	Number of fruits consumed by an individual / hr
<i>Elaeocarpus munroi</i> (Wight) Mast.	SW-pulp	0.48	15.32	25
<i>Ternstroemia gymnanthera</i> (Wight & Arn.) Bedd.	SW-pulp, seed	0.42	28.24	53
<i>Daphniphyllum neilgherrense</i> (Wight) K. Rosenthal	SW-pulp	0.43	6.12	74
<i>Litsea floribunda</i> (Blume) Gamble	SW-pulp, seed	0.47	35.47	25
<i>Cinnamomum macrocarpum</i> Hook.f.	SP	0.31	14.18	72
<i>Vaccinium leschenaultii</i> Wight	SW(P)	0.39	12.45	24
<i>Photinia integrifolia</i> Lindl	SW-pulp, seed	0.45	17.11	13
<i>Syzygium densiflorum</i> Wall. ex Wight & Arn.	SW-pulp	0.37	34.82	100+
<i>Cryptocarya lawsonii</i> Gamble	(P)	0.35	16.47	14
<i>Macaranga peltata</i> (Roxb.) Müll.Arg.	SW-pulp, seed	0.46	18.08	35
<i>Apodytes beddomei</i> Mast.	SW-pulp, seed	0.43	35.69	100+
<i>Turpinia cochinchinensis</i> (Lour.) Merr.	SW-pulp, seed	0.41	5.33	34
<i>Prunus ceylanica</i> (Wight) Miq.	SW-pulp, seed	0.38	6.21	23
<i>Symplocos cochinchinensis</i> (Lour.) S. Moore	SW-pulp, seed	0.34	15.18	43
<i>Viburnum hebanthum</i> Wight & Arn.	SW-pulp, seed	0.44	24.79	103
<i>Symplocos obtusa</i> Wall. ex G.Don	SW-pulp	0.33	0.56	3
<i>Celtis philippensis</i> Blanco	SW-pulp	0.37	2.34	4
<i>Nothapodytes nimmoniana</i> (J.Graham) Mabb.	SW-pulp, seed	0.49	17.22	15
<i>Eurya nitida</i> Korth.	SW-seed	0.38	4.69	4
<i>Syzygium gardneri</i> Thwaites	SP(P)	0.35	3.71	3
<i>Symplocos foliosa</i> Wight	SW-seed	0.36	15.54	13

SW-Swallow, SP-Spit, (P)-Predation



Figure 4.9 A) Fruits fell on the floor during consumption by langur B) Fecal bolus of langur containing the seeds of *Prunus ceylanica* (Wight) Miq.

A total of 161 fecal boluses of Nilgiri langur were collected during the study period (Table), and their analysis indicated the dominance of *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. seeds, which constituted the highest percentage of occurrences (34.98 %), followed by *Mastixia arborea* (Wight) C.B.Clarke (19.81%), *Mastixia arborea* (Wight) C.B.Clarke (14.86%), *Aglaia apiocarpa* (Thwaites) Hiern (13.31%), and *Prunus ceylanica* (Wight) Miq. (10.84%). Although these species dominate their diet, seeds from a variety of other plant species collectively account for 6.19 % of the total occurrences, highlighting a diverse dietary range.

Table 4.8 Major fruit species present in Nilgiri langur fecal bolus (n = 169)

Plant species	Number of occurrences	Percentage of occurrence	Number of intact seeds
<i>Ternstroemia gymnanthera</i> (Wight & Arn.) Bedd.	113	34.98	21
<i>Mastixia arborea</i> (Wight) C.B.Clarke	64	19.81	12
<i>Mastixia arborea</i> (Wight) C.B.Clarke	48	14.86	9
<i>Aglaia apiocarpa</i> (Thwaites) Hiern	43	13.31	8
<i>Prunus ceylanica</i> (Wight) Miq	35	10.84	6
Others (32 species)	<25	6.192	3

Fecal analysis of Nilgiri langurs indicated that *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. was the most frequently observed species with 113 occurrences, accounting for 34.98% of the total, and 21 intact seeds were recovered (Table 8). *Mastixia arborea* (Wight) C.B. Clarke and *Magnolia nilagirica* (Zenker) Figlar were recorded in 64 and 48 samples, respectively, contributing 19.81% and 14.86% of the total occurrences. Both species showed evidence of potential seed dispersal, with 12 and nine intact seeds detected, respectively. In contrast, other fruit species collectively represented a minor portion of the langur diet, with fewer than 25 occurrences each, comprising only 6.19% of the total.

Lion-tailed macaques

The number of lion-tailed macaque sightings was lower than that of Nilgiri langurs. They were almost always in the vicinity of one or another group of Nilgiri langurs throughout their range; the same is not true in the case of Nilgiri langurs. They were observed feeding on the fruits of 20 species belonging to 11 families. The fruits consumed included *Elaeocarpus munroi* (Wight) Mast., *Ternstroemia gymnanthera* (Wight & Arn.) Bedd., and *Litsea floribunda* (Blume) Gamble. Only 12 species were consumed during the maturation stage (Table 9). The remaining specimens were immature. The ENP is usually occupied by three troops of macaques, comprising 9, 15, and 17 individuals. Smaller troops were occasionally encountered, but it was unclear whether they were part of the same troop or belonged to another.

During all observations, the feeding behavioral sequences were of longer duration, with more feeding acts from 10:00-14:00 h. The sequences, hence, were shorter during 14:00-18:00 h (34.01 %) and 6:00-10:00 h (19.13%).

Table 4.9 Fruits consumed by Lion-tailed macaques in ENP

Species	Seed handling	Number of visitation bouts by frugivores/hr	Time spent/visitation bout(min)	Number of fruits consumed by an individual/hr
<i>Elaeocarpus munroi</i> (Wight) Mast.	SW-pulp	0.42	16.24	25
<i>Ternstroemia gymnanthera</i> (Wight & Arn.) Bedd.	SW-pulp, seed	0.46	19.32	30

<i>Meliosma simplicifolia</i> (Roxb.) Walp.	SW-pulp, seed	0.41	12.45	29
<i>Litsea floribunda</i> (Blume) Gamble	SW-pulp, seed	0.48	21.57	35
<i>Magnolia nilagirica</i> (Zenker) Figlar	SW-seed	0.38	14.86	28
<i>Microtropis ovalifolia</i> Wight	SP(P)	0.34	6.42	10
<i>Photinia integrifolia</i> Lindl	SW-pulp, seed	0.45	18.74	29
<i>Syzygium densiflorum</i> Wall. ex Wight & Arn.	SW-pulp	0.47	20.16	38
<i>Casearia thwaitesii</i> Briq.	SP	0.36	3.29	7
<i>Litsea wightiana</i> (Nees) Wall. ex Hook.f.	SW(P)	0.39	14.32	26
<i>Cinnamomum</i> <i>sulphuratum</i> Nees	SP	0.33	7.48	12
<i>Syzygium grande</i> (Wight) Walp.	SW(P)	0.4	15.89	33

SW-Swallow, SP-Spit, (P)-Predation

The average number of visitation bouts by lion-tailed macaques per hour was found to be 0.41 ± 0.05 . The average time spent per visitation bout was observed to average 15.73 ± 3.43 minutes. Additionally, the average number of fruits consumed by an individual per hour was calculated to be 28.66 ± 4.79 .

Due to the limited number of fecal samples collected from macaques, it was not feasible to conduct thorough identification and analysis of the seeds. This constraint hinders our ability to draw conclusive insights into the role of macaques in seed dispersal.

Squirrels (Sciuridae)

The family sciuridae consists of Dusky Striped Squirrel (*Funambulus obscurus*), Western Ghats Striped Squirrel (*Funambulus tristriatus*), Indian Giant Squirrel (*Ratufa indica*), and Grizzled Indian Giant Squirrel (*Ratufa indica*) in Eravikulam National Park. The Indian

Giant Squirrel is a major frugivore that consumed fruits of 31 species (20 families). The dominant families were Lauraceae (5 species) and Myrtaceae (3 species).

R. indica was more active during the morning and evening hours (Fig. 10). The feeding time recorded for the entire study period was 1200 min, including 830 feeding bouts. From 0600 h to 1100 h, feeding was the most dominant activity, and in the afternoon, the feeding activity was highest from 1500 h to 1600 h. A total of 390 (46.98 %) feeding bouts occurred during the forenoon hours, whereas 540 (65.02 %) bouts were recorded in the afternoon. Maximum feeding duration was observed in *Litsea wightiana* (Nees) Wall. ex Hook.f., followed by *Elaeocarpus recurvatus* Corner, *Garcinia cowa* Roxb. ex Choisy, and *Syzygium hemisphericum* (Wight) Alston (Fig. 11).



Figure 4.10 Indian giant squirrel (*Ratufa indica*) in Eravikulam National Park

Table 4.10 Fruits consumed by Indian giant squirrel in ENP

Species	Seed handling	Number of visitation bouts by frugivores/ hr	Time spent/ visitation bout(min)	Number of fruits consumed by an individual/ hr
<i>Ternstroemia gymnanthera</i> (Wight & Arn.) Bedd.	SW-pulp, seed	1.04	17.34	4
<i>Melicope lunu-ankenda</i> (Gaertn.) T.G.Hartley	SP	0.92	15.29	3
<i>Meliosma simplicifolia</i> (Roxb.) Walp.	SW-pulp, seed	0.99	16.21	4
<i>Magnolia nilagirica</i> (Zenker) Figlar	SW-seed	1.15	18.43	5
<i>Palaquium ravii</i> Sasidh. & Vink	SP	0.88	14.79	3
<i>Symplocos foliosa</i> Wight	SP(P)	0.93	15.87	3
<i>Syzygium densiflorum</i> Wall. ex Wight & Arn.	SW-pulp	1.08	17.85	5
<i>Casearia thwaitesii</i> Briq.	SP	0.91	15.12	3
<i>Aglaia apiocarpa</i> (Thwaites) Hiern	SP	0.97	16.04	4
<i>Litsea wightiana</i> (Nees) Wall. ex Hook.f.	SW(P)	1.02	17.12	4
<i>Cinnamomum sulphuratum</i> Nees	SP	0.94	15.76	3
<i>Syzygium hemisphericum</i> (Wight) Alston	SW(P)	1.01	16.97	4

The average number of visitation bouts per hour by Indian giant squirrels was estimated to be 0.98 ± 0.08 . The average time spent per visitation bout was recorded to average 16.50 ± 1.25 minutes. The average number of fruits consumed by an individual per hour was determined to be 3.88 ± 0.67 .



Figure 4.11 A) Fecal samples of squirrel containing seeds of *Elaeocarpus* sp., B) fruits of *Garcinia cowa* Roxb. ex Choisy after consumption by Indian giant squirrel, C) Indian giant squirrel feeding the fruits of the shrub *Maesa indica* (Roxb.) Sweet.

Few intact seeds were found in the fecal samples of *R. indica* because of their seed predation behavior (Table 11).

Table 4.11 Major fruit species present in squirrel fecal samples (n =118)

Plant species	Number of occurrences	Percentage of occurrence	Number of intact seeds
<i>Aglaia apiocarpa</i> (Thwaites) Hiern	17	3.85	4
<i>Symplocos foliosa</i> Wight	12	2.72	7
<i>Elaeocarpus munroi</i> (Wight) Mast.	7	1.59	3
<i>Palaquium ravii</i> Sasidh. & Vink	6	1.36	3
<i>Syzygium hemisphericum</i> (Wight) Alston	2	0.45	0
Others	<25	4.54	1

Civets (Viverridae)

The interaction of civets with fruits in the Shola forests of Eravikulam National Park was recorded using the fruit species identified in fecal samples collected from different locations in the study area. The seeds identified from the fecal sample included *Abarema subcoriacea* (Thwaites) Kosterm., *Pithecellobium subcoriaceum* Thwaites, and *Olea paniculata* R.Br.

A total of 216 fecal samples were collected and analyzed for Shola habitats. More than 52% (n = 112) of fecal samples were collected during the wet season. The Small Indian civet feces were cylindrical in tubes. It was a long, complete piece or broken, segmented, and/or folded into many parts (Fig.12). The small Indian civet was found to use hard surfaces such as rocks and concrete as regular defecation points. Brown palm civet scats are straight, cylindrical (≤ 2 cm in diameter), rounded at both ends, and usually defecated as a single bolus in prominent places, such as fallen logs and rocks, and they showed a more variable defecation habit.



Figure 4.12 Fecal samples of civets from ENP A) during monsoon season, B), C), D), E) post-monsoon season, F) Seeds of Fabaceae sp. remained on the rock after the scat washed off by the rain

The color of the feces varied: dark (48.7%, $n = 105$), brown (27.2%, $n = 59$), red (17.7%, $n = 38$), and green (6.4, $n = 14$). Overall, 84% of the collected feces were solid, whereas 14% were semi-solid. Acacia leaves were observed as a part of a civet diet in this habitat, constituting only 1.9% of the diet. *Abarema subcoriacea* (Thwaites) Kosterm. was observed in 39.16 % of the fecal samples as the main undigested component, followed by *Pithecellobium subcoriaceum* Thwaites (19.58%), and *Palaquium ellipticum* (Dalzell) Baill. (18.18%), and *Elaeocarpus* sp. (11.3%). The number of seeds in each scat varied

from one to 82, with a modal class of 10-15 seeds. Most scats (>95%) contained seeds of only one species (Table).

Table 4.12 Major fruit species present in civet scats (n = 216)

Animal Species	Plant species	Number of occurrences	Percentage of occurrence	Number of intact seeds
Civets 216 samples	<i>Abarema subcoriacea</i> (Thwaites) Kosterm.	56	39.16	45
	<i>Pithecellobium subcoriaceum</i> Thwaites	28	19.58	20
	<i>Palaquium ellipticum</i>	26	18.18	14
	<i>Olea paniculata</i> R.Br.	15	10.49	9
	<i>Elaeocarpus munroi</i> (Wight) Mast.	11	7.69	6
	<i>Microtropis ramiflora</i>	7	4.90	7
	Others (species)	<5	2.10	

Jackals (Canidae)

Similar to civets, the interaction between the golden jackal (*Canis aureus*) and fruits in the Shola forests of ENP was recorded through the collection and identification of fecal samples and the seeds present in them. Golden jackal has been reported to consume 20 species (17 families). The dominant seeds collected from the fecal samples included *Chionanthus mala-elengi* (Dennst.) P.S.Green, *Pithecellobium subcoriaceum* Thwaites, and *Palaquium ravii* Sasidh. & Vink.



Figure 4.13 Fecal samples of golden jackal found in the study area

Intact seeds were extracted from jackal scats (Fig. 13). A total of 80 intact seeds were extracted from 287 scat samples, indicating that many seeds were not damaged through mastication. Of the scats, 50.6% were classified as good germination sites because they were deposited on bushes or shrubs, typically near dirt tracks or trails. Scats deposited on bushes or shrubs eventually fell to the ground, where the fruit seeds were provided with shade. The remainder of the jackal scats were classified as poor germination sites (17.9%) because they were deposited on tufts of grass, or no germination sites (31.5%) because they were deposited on dirt tracks. The defecation sites of jackals consisted of one scat (62.7%), two scats (18.2%), three scats (9.1%), and four to eight scats (10%).

Table 4.13 Major fruit species present in jackal scats (n = 90)

Plant species	Number of occurrences	Percentage of occurrence	Number of intact seeds
<i>Pithecellobium subcoriaceum</i> Thwaites	179	46.02	102
<i>Syzygium hemisphericum</i> (Wight) Alston	86	22.11	34
<i>Litsea wightiana</i> (Nees) Wall. ex Hook.f.	44	11.31	12
<i>Palaquium ravii</i> Sasidh. & Vink	33	8.48	19
<i>Prunus ceylanica</i> (Wight) Miq.	27	6.94	9
<i>Others (15 species)</i>	<25	4.54	

Other frugivorous animals of ENP

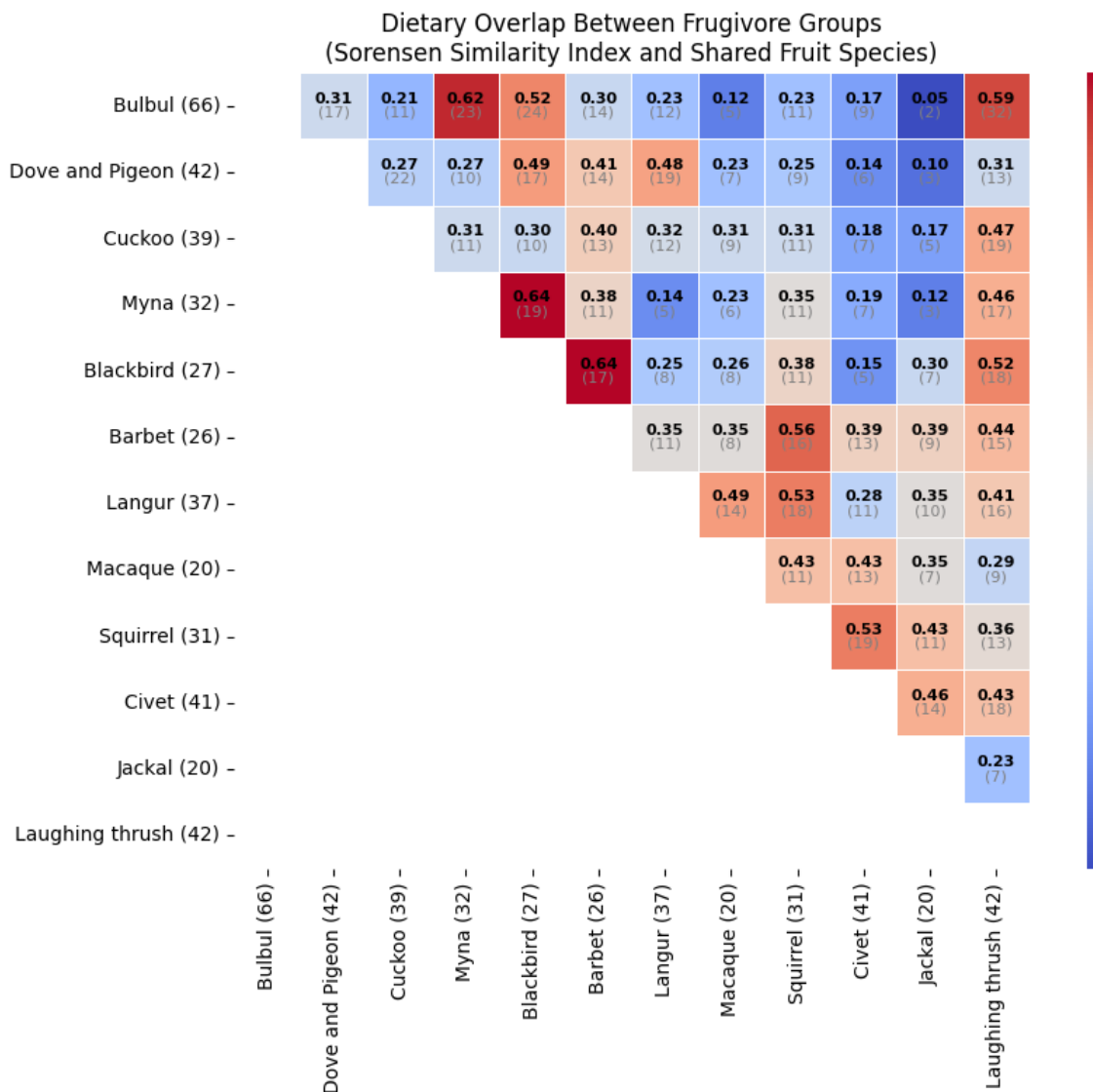
Seven animal species namely the Sloth Bear (*Melursus ursinus*), Indian Elephant (*Elephas maximus*), Wild Boar (*Sus scrofa*), Sambar Deer (*Rusa unicolor*), Barking Deer (*Muntiacus muntjak*), Gaur (*Bos gaurus*), Indian Crested Porcupine (*Hystrix indica*), and Nilgiri Marten (*Martes gwatkinsii*) were observed consuming fruits from various plant species within the park. Fecal samples of *M. ursinus* were found to contain fruits of three species: *Aporosa fusiformis* Thwaites, *Turpinia cochinchinensis* (Lour.) Merr., and *Trichilia connaroides*. Dung from *E. maximus* contained the fruits of *Ternstroemia japonica* (Thunb.) Thunb. and *Ternstroemia gymnanthera* (Wight & Arn.) Bedd.. Fruits of *Ternstroemia japonica* (Thunb.) Thunb, *Ternstroemia gymnanthera* (Wight & Arn.) Bedd., and *Syzygium hemisphericum* (Wight) Alston were identified in fecal samples of *S. scrofa*, *T. connaroides*, and *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. fruits were detected in *R. unicolor* samples, whereas *M. muntjak* primarily consumed *Syzygium hemisphericum* (Wight) fruits. Fruit-deer interaction was identified through analysis of deer tracks and scats, and it was observed that deer regurgitate *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. seeds during rumination.

Dietary overlap between frugivore groups

To analyze the dietary overlap of fruits consumed by frugivores, we grouped frugivores into 12 groups: bulbuls, pigeons and doves, cuckoos, myna, blackbirds, barbet, langur, macaque, squirrel, civet, jackal, and laughing thrush. The number of fruit species consumed by each frugivore group ranged from 4 species consumed by striped-necked mongoose to 45 species consumed by red-whiskered bulbul. We also examined the extent to which different species shared similar food preferences and consumed the same types of resources. Frugivore groups were shared between 2 and 23 fruit species in their diets. Sorensen's similarity index between frugivore groups varied from 0.05 to 0.62 (Table 14). Bulbuls and mynas had a relatively high dietary overlap (similarity index of 0.64), suggesting that they shared a significant number of food items in their diet. There was also a notable dietary overlap between bulbuls and cuckoos (similarity index of 0.59), and Bulbuls and Laughing thrush (similarity index of 0.42). Doves and pigeons showed a moderate dietary overlap with bulbuls (similarity index of 0.31) and cuckoos (similarity index of 0.27). The dietary overlap between the blackbirds and barbets was relatively high (similarity index:0.56). Langurs and Macaques exhibited moderate dietary overlap

(similarity index of 0.41). Squirrels and civets had a dietary overlap (similarity index = 0.43). Jackal showed the least dietary overlap with other species, with a low similarity index with all other species. Observations of nocturnal animals (e.g., civets) were relatively few and their diet lists were likely to be incomplete. It is important to note that these inferences are based solely on the dietary overlap results provided and do not consider other ecological factors or behavioral interactions between the species.

Table 4.14 Dietary overlaps between pairs of consumer groups. The number of fruit species consumed by each frugivore group is shown in parentheses. The dietary overlap values, calculated using Sorensen’s similarity index, are represented by bold numbers. The number of fruit species shared between each pair of groups is shown below Sorensen’s similarity index.



Characteristics of frugivore fruits and seeds

To analyze the characteristics of the fruits consumed by frugivores, we grouped them into 12 groups: bulbuls, pigeons and doves, cuckoos, myna, blackbird, barbet, langur, macaque, squirrel, civet, jackal, and laughing thrush. Frugivores were observed when the fruits of 97 species from ENP were consumed. *Debregeasia longifolia* (Burm.f.) Wedd., *Ternstroemia gymnanthera* (Wight & Arn.) Bedd., *Elaeocarpus munroi* (Wight) Mast., and *Meliosma simplicifolia* (Roxb.) Walp. were the most commonly consumed fruits in the Sholas.

Fruit colour

Bulbul: A strong preference was shown for red (27.8%) and scarlet (25.0%) fruits, with lower consumption observed for brown (13.9%), black (19.4%), and white (11.1%) fruits. Green, blue, pink, and purple fruits were not recorded in the diet.

Pigeon and dove: A wide variety of fruit colors were consumed, with red (20.8%) and black (16.7%) fruits being the most frequent. Blue (16.7%) and brown (12.5%) fruits were also common, whereas yellow, grey, white, and scarlet fruits were consumed less frequently, contributing approximately 2–4% of the total diet.

For the cuckoo, red (25.0%) and scarlet (19.4%) fruits were preferred, followed by brown (19.4%) and black (16.7%) fruits. The other colors were consumed in smaller amounts.

Myna: Red fruits were consumed the most (22.9%), followed by brown and black fruits (17.1% each). Blue, green, and yellow fruits were moderately consumed (8.6% each).

Blackbird: A preference for black (24.2%) and red (24.2%) fruits was evident, with brown (15.2%) and yellow (9.1%) fruits also playing a role in their diet. White, blue, and purple fruits were consumed minimally.

Barbet: Blue fruits (24.0%) were preferred, followed by red (20.0%), black (16.0%), and green (12.0%) fruits. Other fruit colors, such as brown and yellow, were consumed less frequently (8.0% each).

Langur: Brown (20.0%) and grey (20.0%) fruits were favored, and green (16.0%), red (12.0%), and black (8.0%) fruits were consumed. **Macaques:** Brown fruits (26.1%) were consumed most frequently, with moderate amounts of black (17.4%), grey (13.0%), and

red (13.0%) fruits. Green, blue, and yellow fruits were consumed in small amounts (8.7% each).

Squirrels: Brown (22.7%) and red (22.7%) fruits were preferred, whereas black (18.2%) and blue (9.1%) fruits were part of their diet.

Civet: Brown (33.3%) fruits were primarily consumed, followed by red (20.0%) and scarlet (20.0%) fruits. Other colors, such as black, blue, and green, were consumed in smaller quantities.

Jackal: A preference was observed for brown (30.8%) and grey (15.4%) fruits and for black (11.5%) and red (11.5%) fruits. The green, yellow, and blue fruits were consumed in smaller proportions.

Laughing Thrush: Black (24.0%) and red (24.0%) fruits were most frequently consumed, with blue (12.0%), brown (8.0%), and green (8.0%) fruits also included in their diet.

Fruit and seed length and weight

The fruit and seed characteristics of the different frugivore groups exhibited significant variation. Langurs were found to consume the largest fruits, with an average length of 22.18 ± 1.77 mm, followed by squirrels (18.82 ± 2.58 mm) and barbets (16.50 ± 1.13 mm). In contrast, the smallest fruits were consumed by laughing thrushes, with an average length of 9.00 ± 1.04 mm (Fig. 14). Fruit weight also varied significantly, with barbets (4.89 ± 1.03 g) and langurs (4.84 ± 1.10 g) consuming the heaviest fruits, while bulbuls (1.41 ± 0.35 g) and blackbirds (1.28 ± 0.28 g) consumed lighter fruits. Squirrels were found to consume fruits with the heaviest seeds (1.86 ± 0.92 g), whereas bulbuls and laughing thrushes consumed fruits with the lightest seeds (0.47 ± 0.17 g and 0.47 ± 0.19 g, respectively). Seed length was greatest in the fruits consumed by langurs (13.01 ± 1.68 mm), followed by squirrels (12.58 ± 1.97 mm) and jackals (12.13 ± 1.57 mm), while smaller seeds were consumed by species such as bulbuls, blackbirds, and mynas, with average seed lengths of approximately 5–6 mm. Statistically significant differences were observed in fruit length ($F = 6.429$, $P < 0.001$), fruit weight ($F = 2.808$, $P = 0.002$), and seed length ($F = 5.711$, $P < 0.001$) across frugivore groups, whereas seed weight did not vary significantly ($F = 1.348$, $P = 0.198$).

Fruit and Seed Characteristics by Species

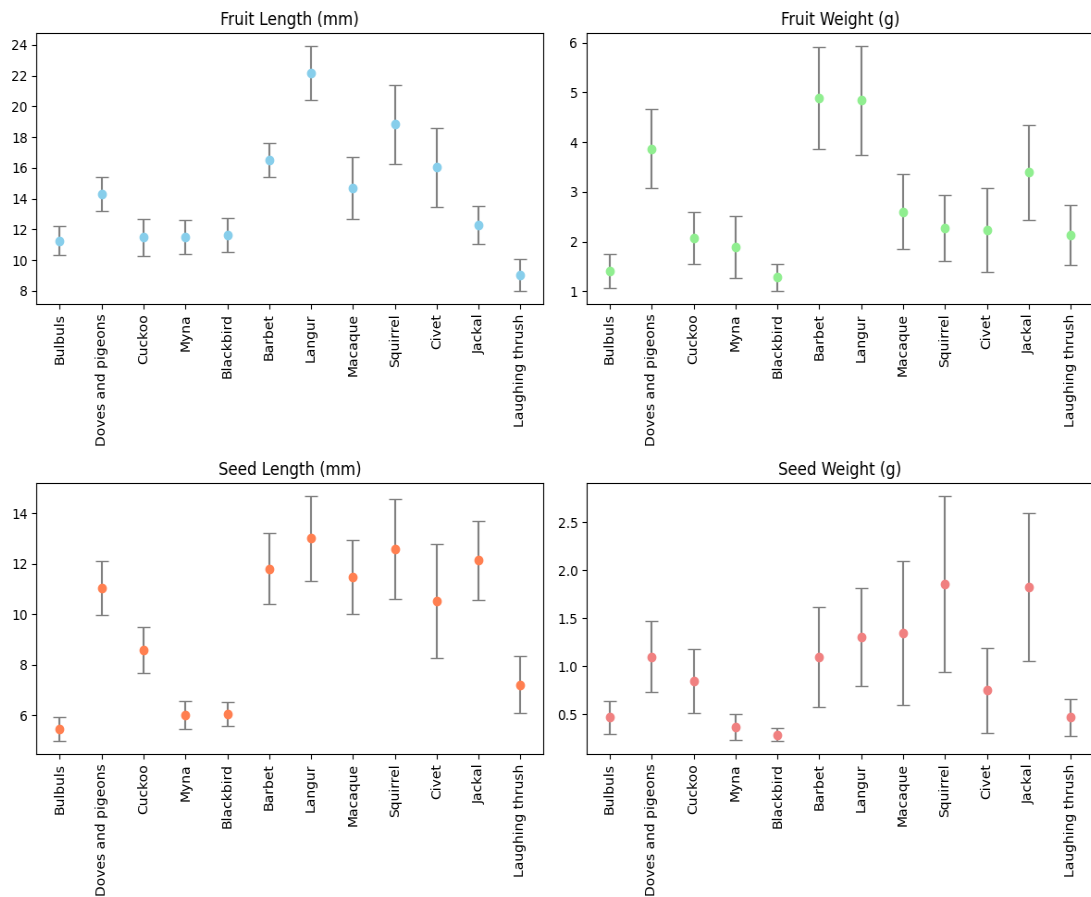


Figure 4.14 Characteristics of fruits and seeds consumed by fruit-eating species in ENP

Interrelation between fruit characteristics

The relationship between fruit characteristics consumed by frugivores showed a positive correlation of 0.121 ($p < 0.05$) between fruit size and fruit weight, suggesting that an increase in fruit size was associated with a slight increase in fruit weight. A positive correlation of 0.409 ($p < 0.01$) was identified between fruit and seed weight, indicating that heavier fruits tend to contain heavier seeds, reflecting a trend in which fruit development influences seed mass. A significant correlation of 0.371 ($p < 0.01$) was found between fruit weight and seed length, implying that larger fruits are likely to have longer seeds and that there is an association between the physical dimensions of the fruit and its seeds. A significant relationship was also noted between seed weight and length, with a correlation of 0.443 ($p < 0.01$), indicating that longer seeds tended to be heavier, which

reflects a consistent pattern of seed morphology. A positive correlation of 0.132 ($p < 0.05$) was identified between fruit size and seed length, suggesting a minor association in which larger fruits may contain longer seeds, although the strength of this relationship is less pronounced.

Influence of frugivores on seed and fruit size dynamics

The minimum number of frugivore groups recorded for a given fruit species was two. Through correlation analysis of the number of frugivores with seed size and fruit size in the Shola forest, the following inferences were drawn: a significant negative correlation was identified between the number of frugivores and seed size (correlation = -0.232, $p = 0.032$). This negative correlation indicates that as the number of frugivores increases, seed size tends to decrease.

Conversely, no significant correlation was observed between the number of frugivores and fruit size (Correlation = -0.054, p -value = 0.767). Consequently, frugivores in Shola forests may not exhibit a strong preference for consuming fruits of particular sizes. This finding implies that frugivores may influence seed selection based on seed size, thereby affecting the seed dispersal patterns and plant regeneration dynamics. In contrast, the absence of a significant correlation between frugivore number and fruit size suggests that frugivores do not selectively choose fruit based on their size.

Observed distribution in the properties of species in the network

A positive correlation was observed between the density and species degree (correlation = 0.615, $p < 0.01$), indicating that higher densities of species were associated with greater degrees of connectivity within the network. Similarly, a positive correlation was found between species strength and density (correlation = 0.561, $p < 0.01$), suggesting that species with greater strength tend to exhibit higher densities. The number of fruit species consumed demonstrated a significant positive correlation with both the species degree (correlation = 1.000, $p < 0.01$) and species strength (correlation = 0.900, $p < 0.01$). These results imply that species that consume a larger variety of fruits are more interconnected and exert a greater influence within the network. Conversely, a significant negative correlation was noted between maximum dependence and the number of fruit species consumed (Correlation = -0.714, $p < 0.01$), indicating that increased reliance on fewer fruit species leads to lower overall dependence. Interaction asymmetry was positively correlated with density (correlation = 0.503, $p < 0.01$) and the number of fruit species

consumed (correlation = 0.819, $p < 0.01$), indicating that species exhibiting greater interaction asymmetry tended to experience higher densities and a broader range of fruit species. Conversely, non-significant correlations were observed for weight, gape width, and other traits, suggesting that these traits do not exhibit a consistent relationship with the properties of the species in the network.

Factors influencing species degree

A regression model was constructed using two predictor variables: Density and Percentage of fruits in the diet. Density and Percentage of fruits in the diet were significant predictors of the degree of species. A positive influence on the species degree was noted for both variables, as evidenced by positive regression coefficients of 2.074 and 0.233, respectively. As the Density and Percentage of fruits in the diet increased, the degree of species tended to increase. The F-value was significant ($p < 0.001$), indicating that the overall model had a good fit for the data. The R-squared value (R^2) was 0.672, suggesting that approximately 67.2% of the variance in the species degree could be explained by the predictors included in the model. This higher R-squared value suggested a relatively good fit for the model. The Durbin-Watson statistic was utilized to test for the presence of autocorrelation in the residuals, with a value close to 2 (2.057) suggesting that there is no significant autocorrelation present in the model's residuals.

Factors influencing species strength

The model was constructed using three predictor variables: Density, Percentage of fruits in the diet, and number of fruit species consumed. Among these predictor variables, the number of fruit species consumed was a highly significant predictor of species strength, as evidenced by its positive regression coefficient of 0.176. As the number of consumed fruit species increased, the species strength tended to increase significantly. In contrast, the Density and Percentage of fruits in the diet were not found to be statistically significant predictors of species strength, as their regression coefficients exhibited relatively low absolute values and their p-values were greater than the significance level of 0.05. The F-value was significant ($p < 0.001$), indicating that the overall model was a good fit for the data. The R-squared value (R^2) was 0.828, suggesting that approximately 82.8% of the variance in species strength could be explained by the predictors included in the model. A higher R-squared value indicates a strong fit of the model. The Durbin-Watson statistic was utilized to test for the presence of autocorrelation in the residuals, with a value close

to 2 (2.398) suggesting that there is no significant autocorrelation present in the model's residuals.

Factors influencing maximum dependence

The model was constructed using three predictor variables: Density, Percentage of fruits in the diet, and number of fruit species consumed. Among these predictor variables, the number of fruit species consumed was a highly significant negative predictor of maximum dependence, as indicated by its negative regression coefficient of -0.016 and a very low p-value (<0.001). As the number of consumed fruit species increased, maximum dependence decreased significantly. In contrast, the Density and Percentage of fruits in the diet were not statistically significant predictors of maximum dependence, as their regression coefficients exhibited relatively low absolute values and their p-values were greater than the significance level of 0.05. The F-value was significant ($p < 0.001$), indicating that the overall model was a good fit for the data. The R-squared value was 0.550, suggesting that approximately 55% of the variance in maximum dependence could be explained by the predictors included in the model. The Durbin-Watson statistic was utilized to test for the presence of autocorrelation in the residuals, with a value of 1.578 indicating the possibility of positive autocorrelation in the model's residuals.

Factors influencing interaction asymmetry

The model included three predictor variables: Density, Percentage of fruits in the diet, and number of fruit species consumed. Among the predictor variables, the number of fruit species consumed was a highly significant positive predictor of interaction asymmetry, as indicated by its positive regression coefficient (0.049) and low p-value (<0.001). As the Number of consumed fruit species increased, interaction asymmetry tended to increase significantly. The density and percentage of fruits in the diet were not statistically significant predictors of interaction asymmetry, as their regression coefficients had relatively low absolute values and their p-values were greater than the significance level of 0.05. The F-value was significant ($p < 0.001$), indicating that the overall model had a good fit for the data. R-squared is 0.780, which means that approximately 78% of the variance in the Interaction asymmetry can be explained by the predictors (Density, Percentage of fruit in the diet, and Number of fruit species consumed) included in the model. The Durbin-Watson statistic test for the presence of autocorrelation in the residuals

was 2.274. The value was close to two, indicating no significant autocorrelation in the residuals of the model.

Seed germination studies

In total, 600 fecal samples were examined in this study. Of these, 35.3% contained seeds/fruits or seedlings of woody species, 56.4% (n=338) contained seeds only, and 3.0% contained seedlings only. Seeds and seedlings were found in 10.6% of fecal samples. Most fecal samples (63.9%) from a single defecation contained seeds or seedlings of a single species. The seed number was high in dung during the monsoon season (Fig. 15). Few seeds were found in November, December, and January.

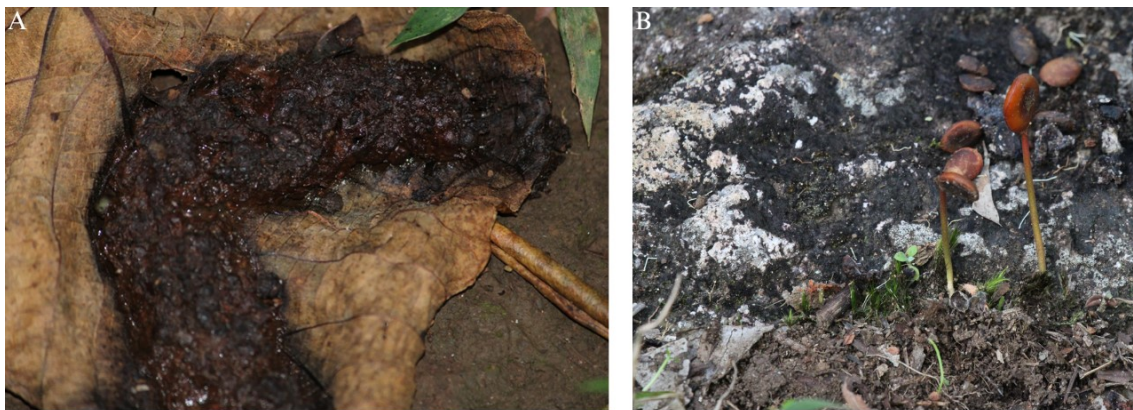


Figure 4.15 A) Fecal sample of Macaques containing seeds, B) Civet scat containing germinated seeds of *Abarema subcoriacea* (Thwaites) Kosterm. found near Erachippara waterfalls

Altogether, 879 seeds belonging to 19 species (with three unidentified species) were recovered from 593 fecal samples. The most abundant seeds were *Pithecellobium subcoriaceum* Thwaites (179), and *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. (113), and *Syzygium hemisphericum* (86). Of the fecal samples, 60.37% contained intact seeds (Fig. 16). Very few seeds germinated during the germination experiment. These germinated seeds showed that more ingested seeds germinated than the control, except for *Syzygium hemisphericum* (Wight) Alston. On average it took 25.8 ± 4.2 days taken for the ingested seeds to germinate. It took an average of 31.4 ± 404 days for the control seeds (seeds collected from the plant) to germinate.



Figure 4.16 A) Fecal sample of Sloth bear containing seeds of unidentified species, seeds of B) *Mahonia leschenaultii* (Wall. ex Wight & Arn.) Anon., C) *Abarema subcoriacea* (Thwaites) Kosterm., D) *Magnolia nilagirica* (Zenker) Figlar, E) *Elaeocarpus munroi* (Wight) Mast., F) *Ternstroemia gymnanthera* (Wight & Arn.) Bedd., G) *Rhodomyrtus tomentosa* (Aiton) Hassk. (shrub), H) *Palaquium ellipticum* (Dalzell) Baill., I) germination experiment containing control seeds and seeds collected from fecal sample after animal gut passage, J) germinated seedlings.

4.4 | DISCUSSION

Frugivores in ENP

Avian frugivores

The tropical montane forest of Eravikulam National Park is dominated by five species of bulbuls: Nilgiri wood pigeon, Palani laughing thrush, Nilgiri langur, blackbird, lion-tailed macaque, golden jackal, small Indian civet, and four squirrel species. The most important Shola forest fruit-eating species were the red-whiskered bulbul, myna, Nilgiri wood pigeon, and Palani laughing thrush. The high number of interactions between bulbul and plant species supports the idea that abundant species are more likely to interact with several plant species (Bascompte and Jordano, 2007; Sanitjan and Chen, 2009; Vázquez et al., 2009a). Bulbuls were the most abundant birds in ENP, particularly the red-whiskered bulbul, which likely accounts for the higher fruit consumption rate than that observed in other frugivores that occur at lower densities. When feeding on fruits, bulbuls typically swallow them and carry seeds in their guts, which could have additional positive effects on germination (Corlett, 1998b). Red-whiskered bulbuls (*P. jocosus*) in Reunion Island could defecate up to 2,000 *Clidemia hirta* seeds per dropping. This evidence suggests that bulbuls can be effective seed dispersers of both native and exotic plants (Mandon-dalger et al., 2004).

Seed dispersal by Nilgiri wood pigeons has been reported in other tropical ecosystems in India, such as Nilgiri wood pigeon dispersing the fruits of 39 species in the Western Ghats, India (Sellamuthu and Lalitha, 2010), and seed dispersal by Nilgiri wood pigeon in Kalakad–Mundanthurai Tiger Reserve, southern India (Ganesh and Davidar, 2001). Due to their large gape width (1.83–1.84 cm), Nilgiri wood pigeons were able to consume larger-sized fruits and seeds. The Nilgiri laughingthrush is endemic to the Western Ghats and is frequently seen foraging in small groups, playing a relevant role as a potential seed disperser.

The broader frugivore community, including species such as the black-hooded oriole (*Oriolus xanthornus*), Indian lorikeet (*Trichoglossus chlorolepidotus*), and Asian fairy-bluebird (*Irena puella*), illustrates the richness of bird-plant interactions within the ENP. Variation in fruit preferences and feeding strategies across species reflects functional diversity, which likely enhances seed dispersal efficiency across spatial scales. These findings align with earlier research on tropical and subtropical forests, which emphasized

the role of avian frugivores in shaping plant community structures through seed dispersal (Herrera, 2002).

Mammalian frugivores

The documented frugivorous behavior of major animals such as Nilgiri langurs, lion-tailed macaques, Malabar giant squirrels, civets, and jackals demonstrates their diverse interactions with fruits and seeds from a wide range of plant species. These findings underscore the importance of understanding plant-animal interactions, as the behavior of these animals affects seed survival, dispersal patterns, and ultimately, plant regeneration (Corlett, 2017; Campos-Arceiz and Blake, 2011). The results indicate that Nilgiri langurs and lion-tailed macaques are key frugivores with distinct seed handling strategies such as seed spitting, swallowing, and predation. These behaviors are consistent with previous studies on primate-mediated seed dispersal, where large-bodied primates serve as effective dispersers, especially for large seeds that cannot be dispersed by smaller frugivores (Janson, 1983; Lambert, 2002). This study further confirms that langurs play a dual role as both dispersers and seed predators, depending on the species of fruit consumed, which aligns with existing research on primate fruit preferences and seed treatments (Kaplin and Lambert, 2002). The frugivory of the Malabar giant squirrel contributes to seed dispersal in the ENP, particularly for species in the Lauraceae and Myrtaceae families. This finding mirrors previous research that has shown squirrels to be important seed dispersers and predators, with feeding activity often varying to avoid competition with other frugivores (Steele et al., 2005). The observed variation in feeding times and fruit preferences across species supports studies of the temporal partitioning of feeding activity by frugivores to optimize resource use (Vázquez and Simberloff, 2003). Civets and jackals also play significant roles as secondary seed dispersers, as evidenced by intact seeds recovered from their fecal samples. The use of prominent defecation sites by civets and jackals further enhances the spatial distribution of seeds, often in microhabitats conducive to seed germination, corroborating the findings of other carnivore-mediated seed dispersal studies (Herrera, 1989; Wang & Smith, 2002). The defecation habits of these species create seed dispersal networks that can benefit forest regeneration by promoting seed deposition in shaded or nutrient-rich areas (Farwig and Berens, 2012).

Dietary overlap between frugivore groups

The findings revealed significant dietary overlap among certain frugivores, such as bulbuls, mynas, and cuckoos, suggesting shared foraging strategies and similar food preferences. These overlaps align with previous studies, which reported that generalist frugivores such as bulbuls and mynas often consume a wide variety of fruits, contributing significantly to seed dispersal (Jordano et al., 2007; Corlett, 2017). The high similarity between these groups may also suggest potential competition during periods of fruit scarcity, which can affect the role of both species as seed dispersers.

Interestingly, the moderate overlap between langurs and macaques and between squirrels and civets reflects the partial dietary specialization of these species, which allows them to coexist while reducing direct competition for resources. Previous studies have shown that primates, such as langurs and macaques, exhibit selective fruit preferences, which vary seasonally and spatially, influencing seed dispersal patterns (Lambert, 2002; Kaplin and Lambert, 2002). The overlap between squirrels and civets, though moderate, emphasizes their complementary roles as seed dispersers, with squirrels often acting as seed predators and dispersers, whereas civets predominantly disperse intact seeds through defecation (Steele et al., 2005; Wang and Smith, 2002).

The low dietary overlap of the jackal with other frugivores suggests a more distinct ecological niche, possibly because of its omnivorous diet and different foraging behaviors, contributing to seed dispersal through a mechanism different from that of other frugivores (Wang and Smith, 2002). This limited overlap indicates that jackals play a unique role in dispersing particular fruit species, especially those less targeted by more specialized frugivores.

Characteristics of frugivore fruits and seeds

The observed variation in fruit color preferences across frugivore groups reflects the diverse foraging strategies and visual sensitivities of these species. For example, the strong preference of bulbuls and blackbirds for red and black fruits aligns with previous studies, which suggests that these colors are particularly attractive to avian frugivores because of their enhanced visibility against green foliage (Burns, 2015). This preference for visually conspicuous fruits suggests that plants producing brightly colored fruits may have evolved in response to frugivore selection, thereby enhancing their chances of seed dispersal (Jordano, 2007).

The differences in fruit and seed sizes consumed by different frugivores further highlight the diversity of frugivory strategies. Langurs and squirrels, which consume large fruits and seeds, are likely to play a crucial role in the dispersal of large-seeded species. These findings confirm previous research, which has shown that larger frugivores tend to consume and disperse larger fruit seeds, often over longer distances, contributing significantly to the forest structure and composition (Howe and Miriti, 2004; Kitamura et al., 2002). In contrast, smaller frugivores, such as bulbuls and laughing thrushes, which consumed lighter fruits with smaller seeds, are more likely to disperse small-seeded plants, which may lead to a higher density of plant recruitment in the immediate vicinity (Jordano et al., 2007).

The significant correlations between fruit size, seed size, and seed weight indicated that fruit morphology plays an integral role in seed dispersal dynamics. The positive relationship between fruit and seed weight suggests that larger fruits tend to harbor heavier seeds, which may influence dispersal effectiveness (Wheelwright, 1985). However, the negative correlation between the number of frugivores and seed size indicates an interesting trend, where fruits with smaller seeds are consumed by a greater diversity of frugivores. This supports the idea that smaller-seeded species may rely on a broader array of dispersers, potentially enhancing their chances of successful dispersal (Song et al., 2022).

The lack of a significant correlation between frugivore number and fruit size suggests that frugivores in Shola forests do not exhibit strong size preferences for fruits, which contrasts with some prior studies where frugivores displayed preferences for specific fruit sizes (Jordano et al., 2007). This discrepancy may reflect the unique ecological conditions of the Shola forests or the adaptability of frugivores to available fruit resources, indicating the need for further research on the temporal availability of fruit and its influence on frugivore behavior.

Observed distribution in the properties of species in the network

A positive correlation between species density and degree as well as species strength suggests that higher species densities contribute to greater connectivity and influence within the network. This finding is consistent with previous studies, which highlight that species with higher densities are more likely to engage in multiple interactions, thereby increasing their ecological significance in seed dispersal networks (Bascompte and

Jordano, 2007; Schleuning et al., 2015). These highly connected species, particularly those with high species strength, play a critical role in maintaining the structure and function of seed-dispersal systems by facilitating the spread of seeds across the ecosystem.

The significant positive correlation between the number of fruit species consumed and both species degree and species strength indicates that frugivores that consume a wider variety of fruits are more interconnected and influential in the network. This supports the notion that generalist species, which interact with multiple plant species, enhance the stability and resilience of seed-dispersal networks (Mello et al., 2011). By consuming diverse fruit species, these generalist frugivores contribute to greater plant recruitment, thereby promoting plant diversity and ecosystem resilience (Jordano, 2007).

The negative correlation between maximum dependence and the number of fruit species consumed suggests that species with a broader diet are less dependent on a specific fruit species. This inverse relationship aligns with the theory that generalists are more adaptable and less vulnerable to fluctuations in fruit availability, making them key players in maintaining seed dispersal functions during periods of resource scarcity (Olesen et al., 2008). Conversely, species with a higher dependence on fewer fruit species may be more vulnerable to changes in fruiting patterns, potentially affecting their role in seed dispersal (Blüthgen et al., 2007).

Interestingly, the non-significant correlations between physical traits, such as weight and gape width, and network properties suggest that these morphological characteristics may not play a major role in determining frugivore connectivity within the network. This contrasts with some studies that have emphasized the importance of morphological matching between frugivores and fruits (Dehling et al., 2014). However, the lack of significance in this study may reflect the diverse foraging strategies and adaptability of frugivores in the Shola forests, indicating that other factors, such as behavioral traits or fruit abundance, may play a more critical role in shaping interactions. Regression analysis reinforces the importance of species diets in influencing the network properties. The number of fruit species consumed emerged as the strongest predictor of species strength and interaction asymmetry, indicating that frugivores with broader diets exert a disproportionate influence on the network. This confirms earlier research, which found that frugivores with broader diets enhance the stability of seed dispersal networks by

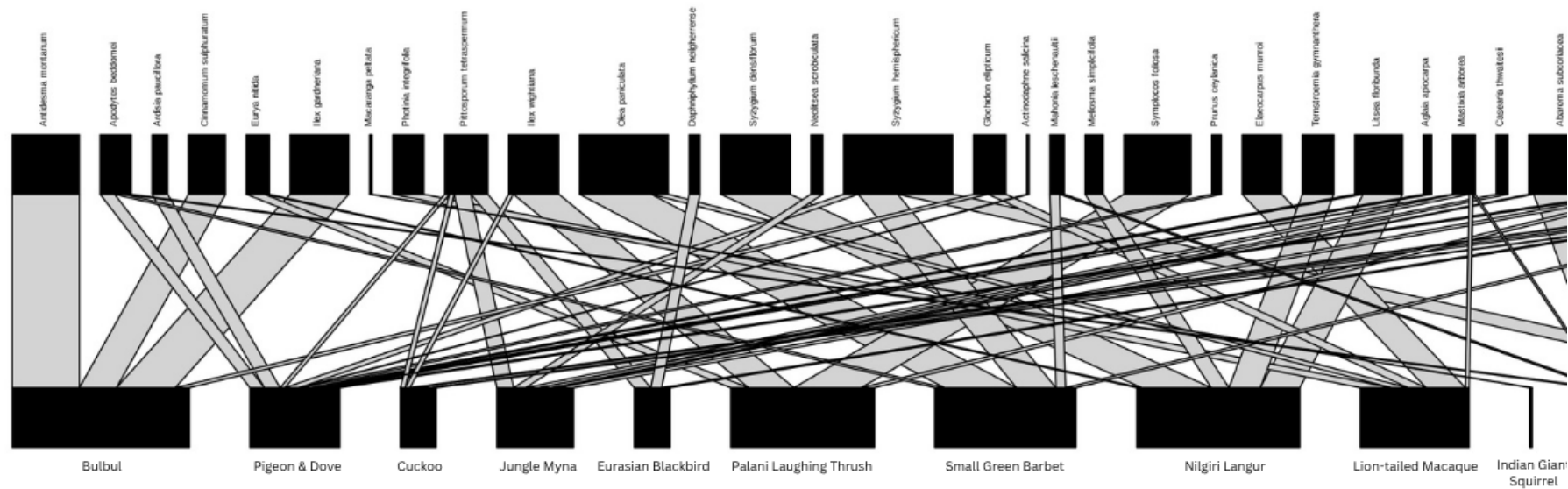


Figure 4.17 Bipartite plant - frugivore network construction of quantitative observation network. Plant species are given in the upper boxes, and frugivore species in the lower boxes. Lines represent weighted interaction frequencies between frugivore and plant species

reducing dependence on individual plant species and promoting a more even distribution of dispersal events (Schupp et al., 2010). In contrast, while density was a significant predictor of species degree, it was not a strong predictor of species strength or interaction asymmetry, suggesting that while density contributes to connectivity, dietary diversity is more crucial for determining a frugivore's ecological influence.

These findings emphasize the pivotal role of generalist frugivores in maintaining network stability and plant diversity, as well as the importance of considering both behavioral and ecological factors when assessing the structure and function of these networks. Understanding frugivore visitation and seed handling informs restoration practices, such as selecting tree species that attract generalist dispersers, rewilding frugivore populations, and prioritizing corridors that maintain plant–animal interactions. Future studies should explore the temporal dynamics of these interactions and assess how seasonal variations in fruit availability influence the role of frugivores in seed dispersal.

4.5 | IMPLICATIONS FOR CONSERVATION

The findings of this study have critical implications for conservation efforts in Shola forests and similar ecosystems. Promoting frugivore diversity is essential because generalist frugivores that consume a wide variety of fruits play a key role in maintaining network stability and seed dispersal (Jordano, 2007; Mello et al., 2011). Habitat restoration and enhancement of landscape connectivity are vital for facilitating frugivore movement and promoting interactions between species (Haddad et al., 2015). Moreover, managing the availability of diverse fruit resources throughout the year will support frugivore populations and mitigate their dependence on a limited number of fruit species, thereby promoting resilience (Schupp et al., 2010). Integrating knowledge of frugivore-plant interactions into conservation planning can enhance efforts to protect key species and their habitats (Blüthgen et al., 2007). Finally, ongoing monitoring and research on frugivore dynamics will inform adaptive management strategies in response to emerging threats (Schleuning et al., 2015).

4.6 | CONCLUSION

In conclusion, this study provides valuable insights into the complex interactions between frugivores and fruiting plants within Shola forests, highlighting the intricate dynamics of seed dispersal and plant-animal interactions. The observed dietary overlap among

frugivores underscores the significance of species diversity in maintaining ecological balance and promoting effective seed dispersal. The relationships between fruit and seed characteristics reveal how frugivores influence the evolution of fruit traits and seed morphology, thereby affecting plant regeneration processes. Furthermore, network analysis illustrated the importance of connectivity among frugivore species, emphasizing their role in the overall health and stability of the ecosystem. By integrating these findings into conservation strategies, we can enhance our efforts to preserve biodiversity, promote habitat restoration, and ensure the sustainability of frugivore populations, ultimately contributing to the resilience of forest ecosystems. Future research is essential to deepen our understanding of these interactions and adapt conservation practices to the evolving challenges faced by this critical ecological network.

4.7 | RECOMMENDATIONS

1. Prioritize the conservation of Shola forests and their surrounding ecosystems to maintain the biodiversity of frugivores and fruiting plants, focusing on reestablishing native species that serve as food sources.
2. Implementation of long-term monitoring programs to assess the health and dynamics of frugivore populations, providing data that can inform effective conservation strategies.
3. Develop wildlife corridors to connect fragmented habitats, facilitating movement and interaction among frugivore species and promoting genetic diversity.
4. Local communities should be involved in conservation efforts by raising awareness of the ecological significance of frugivores and their role in seed dispersal, fostering sustainable land-use practices.

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Appendix 2. Frugivores observed in Eravikulam National Park with their body mass, number of species of fruits consumed, frugivore density in square kilometre area, total number of visits made by frugivores, and average visits length(during each observation bout).

Family	Common name	Scientific name	Weight (g)	No. of fruit species consumed	Density (inds /km ²)	Total number of visits	Average visit length (min)
Megalaimidae	Small Green Barbet	<i>Megalaima viridis</i>	90	26	2.02	72	7.30
Cuculidae	Indian Cuckoo	<i>Cuculus micropterus</i>	120	20	2.72	89	2.11
Cuculidae	Lesser Coucal	<i>Centropus bengalensis</i>	150	29	0.78	57	1.65
Columbidae	Nilgiri Wood Pigeon	<i>Columba elphinstonii</i>	380	38	1.02	27	3.05
Turdidae	Eurasian Blackbird	<i>Turdus merula</i>	100	27	7.2	183	.82
Corvidae	Large-billed Crow	<i>Corvus macrorhynchos</i>	1000	20	0.48	14	1.10
Sturnidae	Jungle Myna	<i>Acridotheres fuscus</i>	98	32	12.8	315	0.56
Pycnonotidae	Gray-headed Bulbul	<i>Brachypodius priocephalus</i>	19	20	9.46	78	0.73
Pycnonotidae	Red Whiskered Bulbul	<i>Pycnonotus jocosus</i>	28	48	16.38	478	1.9
Pycnonotidae	Red Vented Bulbul	<i>Pycnonotus cafer</i>	45	37	12.1	380	1.8
Pycnonotidae	Yellow Browed Bulbul	<i>Iole indica</i>	34	16	7.23	64	1.14
Pycnonotidae	Black Bulbul	<i>Hypsipetes leucocephalus</i>	40	20	1.26	29	0.68
Leiothrichidae	Palani Laughingthrush	<i>Montecincla fairbanki</i>	n/a	42	11.71	281	0.63
Cercopitheciidae	Nilgiri Langur	<i>Semnopithecus johni</i>	11921	37	4	256	7.64

Viverridae	Small Indian Civet	<i>Viverricula indica</i>	2908.4	24	3.1	24	1.02
Canidae	Golden Jackal	<i>Canis aureus</i>	10345.2	20	n/a	4	0.56
Viverridae	Brown Palm Civet	<i>Paradoxurus jerdoni</i>	3156.7	31	7.8	37	0.51
Sciuridae	Dusky Striped Squirrel	<i>Funambulus sublineatus</i>	70.9	20	2.2	25	0.42
Sciuridae	Western Ghats Striped Squirrel	<i>Ratufa indica maxima</i>	1060	31	4	40	0.38
Columbid ae	Spotted Dove	<i>Streptopelia chinensis</i>	160	20	2.14	32	1.16
Columbid ae	Jerdon's Imperial Pigeon	<i>Ducula badia</i>	500	22	0.56	6	4.64
Cercopithecidae	Lion Tailed Macaque	<i>Macaca silenus</i>	4750	20	0.5	17	6.86
Minor frugivore							
Phasianidae	Jungle Bush Quail	<i>Perdica asiatica</i>	65	4	0.84	19	0.25
Phasianidae	Grey Jungle fowl	<i>Gallus sonneratii</i>	1140	4	6.48	17	0.27
Cuculidae	Crow Pheasant	<i>Centropus sinensis</i>	240	12	2.01	15	0.86
Psittaculidae	Indian Lorikeet	<i>Loriculus vernalis</i>	36	4	0.04	2	0.45
Columbid ae	Emerald Dove	<i>Chalcophaps indica</i>	171	12	0.89	13	0.74
Columbid ae	Green Imperial Pigeon	<i>Ducula aenea</i>	645	19	0.25	21	4.17
Irenidae	Asian Fairy-bluebird	<i>Irena puella</i>	75	5	0.81	3	1.04
Oriolidae	Black-hooded Oriole	<i>Oriolus xanthornus</i>	56	8	1.2	16	1.29

Campeph agidae	Orange Minivet	<i>Pericrocotus flammeus</i>	25	7	0.84	23	1.31
Vangidae	Bar-winged Flycatcher-shrike	<i>Hemipus picatus</i>	10	4	0.42	2	0.9
Dicrurida e	Fork-tailed Drongo	<i>Dicrurus adsimilis</i>	40	4	1.07	6	0.56
Dicrurida e	Ashy Drongo	<i>Dicrurus leucophaeus</i>	55	7	1.26	23	0.71
Aegithini dae	Common Iora	<i>Alghina tiphia</i>	13	6	1.42	13	0.63
Muscicapi dae	Malabar Whistling Thrush	<i>Myiophonus horsfieldii</i>	130	16	4.02	76	1.23
Turdidae	Pied Thrush	<i>Geokichla wardii</i>	72	4	0.32	5	0.66
Turdidae	Nilgiri Thrush	<i>Zoothera neilgherriensis</i>	50	4	0.51	4	0.79
Muscicapi dae	White-bellied Sholakili	<i>Sholicola albiventris</i>	30	7	0.37	23	2.19
Muscicapi dae	Black-and-orange Flycatcher	<i>Ficedula nigrorufa</i>	10	6	0.77	20	1.42
Muscicapi dae	Verditer Flycatcher	<i>Eumyias thalassinus</i>	20	4	0.48	2	0.71
Muscicapi dae	Nilgiri Flycatcher	<i>Eumyias albicaudatus</i>	19	7	5.3	218	1.14
Muscicapi dae	White Bellied Blue Flycatcher	<i>Cyornis pallidipes</i>	23	10	2.47	49	1.26
Muscicapi dae	Oriental Magpie- Robin	<i>Copsychus saularis</i>	36	8	1.2	12	0.96
Sittidae	Velvet Fronted Nuthatch	<i>Sitta frontalis</i>	17	4	0.69	4	0.49
Paridae	Great Tit	<i>Parus major</i>	22	16	4.09	26	0.83

Paridae	Yellow Cheeked Tit	<i>Machlolophus spilonotus</i>	23	9	4.85	31	0.79
Cisticolidae	Ashy Prinia	<i>Prinia socialis</i>	10	4	0.62	4	0.46
Cisticolidae	Plain Prinia	<i>Prinia inornata</i>	9	7	1.13	7	0.42
Zosteropidae	Indian White-eye	<i>Zosterops palpebrosa</i>	10	5	0.54	11	1.01
Locustellidae	Common Grasshopper Warbler	<i>Locustella naevia</i>	13	4	0.82	3	1.43
Locustellidae	Broad-tailed Grassbird	<i>Schoenicola platyurus</i>		4	0.23	12	1.54
Phylloscopidae	Greenish Leaf Warbler	<i>Phylloscopus trochiloides</i>	8.1	5	0.47	15	1.36
Phylloscopidae	Large Billed Leaf Warbler	<i>Phylloscopus magnirostris</i>	13	5	2.03	15	2.14
Leiothrichidae	Rufous Babbler	<i>Argya subrufa</i>	78	6	6.34	11	1.06
Timaliidae	Indian Scimitar-babbler	<i>Pomatorhinus horsfieldii</i>	53	5	6.03	3	1.89
Dicaeidae	Thick Billed Flower Pecker	<i>Dicaeum agile</i>	9	4	0.12	11	0.61
Dicaeidae	Nilgiri Flower Pecker	<i>Dicaeum concolor</i>	8	4	5.13	7	0.52
Nectariniidae	Crimson-backed Sunbird	<i>Leptocoma minima</i>	6	4	n/a	8	0.39
Fringillidae	Common Rose finch	<i>Carpodacus erythrinus</i>	24	4	n/a	5	0.79
Ursidae	Sloth Bear	<i>Ursus ursinus</i>	93130	9	n/a	2	n/a
Elephantidae	Indian Elephant	<i>Elephas maximus</i>	4000000	7	n/a	6	n/a

Suidae	Wild Boar	<i>Sus scrofa</i>	101052.1	10	3.69	4	n/a
Cervidae	Sambar Deer	<i>Rusa unicolor</i>	180344.4	5	1.49	2	n/a
Cervidae	Barking Deer	<i>Muntiacus muntjack</i>	15925.8	6	0.1	9	n/a
Bovidae	Gaur	<i>Bos gaurus</i>	1000000	6	1.3	42	n/a
Mustelidae	Nilgiri Marten	<i>Martes gwatkinsi</i>	2043	4	0.2	1	n/a
Herpestidae	Indian Grey Mongoose	<i>Herpestes edwardsi</i>	1324.2	4	1.2	4	n/a
Herpestidae	Ruddy Mongoose	<i>Herpestes smithi</i>	1982	6	0.3	1	2.14
Herpestidae	Indian Brown Mongoose	<i>Herpestes fuscus</i>	2700	5	3.3	1	3.16
Herpestidae	Striped Necked Mongoose	<i>Herpestes vitticollis</i>	2575.6	4	0.7	2	4.12
Sciuridae	Jungle palm squirrel	<i>Funambulus tristriatus</i>	139	8	4	6	0.88
Sciuridae	Grizzled Indian Giant Squirrel	<i>Ratufa macroura</i>	1327.1	7	1.9	2	1.36
Hystriidae	Indian Crested Porcupine	<i>Hystrix indica</i>	12435.8	16	6.8	17	3.96

Seasonal variation in fruit biomass production in Shola forests of Eravikulam National Park

ABSTRACT

This chapter examines fruit biomass production in Shola forests, with special emphasis on dispersal syndromes. This study measured fruit biomass production across years and months. The fruit biomass data were compared with the seasons and seed dispersal syndromes. Our results indicated an average fruit biomass of 384.69 kg/ha/y, a minimum biomass of 320.69, and a maximum recorded biomass of 443.95 kg/ha/y. The biomass production recorded from Shola forests was comparable to that recorded from other moist altitudinal forests but lower than that recorded in several tropical and subtropical regions. A significant portion of biomass production in Shola forests of ENP is contributed by large fruits that are often dispersed by frugivorous birds and animals, despite the lower abundance of large fruits comparable to that of smaller fruits in this ecosystem. Analysis of fruit biomass production across seasons, such as the wet and dry seasons, and across months, revealed a significant fruiting peak during the wettest months of the year during the monsoon period, providing a suitable microclimate for germination and seedling establishment. Our findings align with the germination hypothesis that connects optimal seed germination with prolonged wet conditions. Analysis of fruit production at varying temperatures indicated a positive correlation between fruit production and the minimum temperature. These observations suggest that factors such as rainfall availability and temperature synergistically influence fruit biomass production in the Shola forests. Peak fruit production during the months of rainfall further increases the significance of fruit biomass production in Shola, which can provide diverse frugivore communities in this unique ecosystem. The intricate relationships between frugivore diets discussed in the previous chapter and the fruiting patterns discussed here highlight the importance of understanding how these factors function together to facilitate ecosystem resilience. In this chapter, we attempt to understand in detail the patterns of fruiting phenology in Shola forests and establish a baseline for future research. Long-term in-depth phenological

research is required to understand the processes that control reproductive events. This knowledge is essential for developing conservation initiatives aimed at maintaining the ecological integrity of tropical montane forests.

5.1 | INTRODUCTION

Tropical forests are seasonal environments that are characterized by complex patterns of plant reproduction (Sabatier, 1985). These reproductive events shape the composition of vegetation and can have lasting impacts on forest structure, dynamics, and regeneration. Fruiting and seeding cycles determine the seed deposition patterns and shape the spatial distribution of plant species in different habitats (Schupp et al., 2002; Silvius and Fragoso, 2003). Consequently, the temporal and spatial patterns of fruit and seed production are important determinants of forest regeneration and structural heterogeneity (Schupp, 1990). Tropical plant communities often exhibit significant spatial and temporal variations in fruit production (Chapman et al., 2005; van Schaik and Pfannes, 2005). These patterns are influenced by abiotic factors such as rainfall, temperature, soil type, and photoperiod (Silva et al., 2011; Carvalho and Sartori, 2015; Clark et al., 1998; Pezzini et al., 2014), as well as by biotic variables like the abundance and activity of pollinators and seed dispersers (Chapman et al., 1999, 2018; Wheelwright and Orians, 1982). Fruit fall data has proven useful in estimating the regenerative capacity of trees following disturbance and in assessing geographical variation in reproductive output (Terborgh, 1990).

Frugivore assemblages and behaviour can be significantly impacted by these localised patterns of fruit production. Within the forest ecosystem frugivore diet, foraging habitat and assemblages are impacted by variations in fruit availability (Loiselle and Blake, 1990; Van Schaik et al., 1993; Peres, 1994). As nearly 90 percent of fleshy fruits depend on animals to disperse their seeds in the tropics (Jordano, 2000), the study of the fruiting patterns can provide insights into the specific plant-animal interaction demographic consequences of variation in seed production. Quantifying fruit biomass enables the analysis of these associations between fruiting variation and frugivore activity cycles (Levey et al., 1993). As a result, fruit biomass variability can serve as an indicator of habitat productivity and quality (Chapman et al., 1994; Worman and Chapman, 2006). Annual estimates of fruit biomass support the assessment of forest productivity and inform conservation strategies aimed at sustaining frugivore populations (Snyder et al., 1987).

The present study represents the first systematic assessment of fruit biomass production within the Shola forests of the Western Ghats. While earlier studies have primarily concentrated on fruit production estimates from individual tree species, this research adopts a community-level approach. Given the critical ecosystem services provided by frugivores particularly their role in seed dispersal it becomes essential to quantify overall fruit production, investigate its seasonal variability, and evaluate its influence on frugivore assemblages and activity.

Seasonal changes in fruit availability were documented as part of a broader research initiative focused on seed dispersal dynamics in Eravikulam National Park (ENP). As part of this effort, the spatial distribution of woody species was also mapped. The central aim of the present study was to measure monthly fluctuations in both the number of fruiting individuals and the biomass of fruits produced, particularly among species dispersed by various seed dispersal mechanisms. Through the analysis of fruit production patterns, this work seeks to advance our understanding of high-elevation forest ecology and emphasize the ecological relevance of fruit biomass in sustaining the biodiversity and functional stability of Shola ecosystems.

This investigation is embedded within a larger seed dispersal framework, and it extends beyond phenology to explore the nutritional attributes of fruits consumed by frugivores. Understanding these characteristics can shed light on foraging preferences and disperser effectiveness, thereby enriching our comprehension of plant-animal mutualisms.

The specific objectives of this study were to:

1. Quantify fruit biomass production in the tropical montane forests of Eravikulam National Park.
2. Analyze the fruiting patterns available in tropical montane evergreen forests of the Eravikulam National Park.
3. Characterize the variations in fruiting availability with respect to season and dispersal mode.
4. Examine the nutritional characteristics of fruits consumed by frugivores.

Finally, the study discuss the possible consequences of fruit availability for animal communities at this forest site in the Eravikulam National Park. By addressing these research goals, the chapter aims to generate insights into the ecological role of fruit

biomass production and inform evidence-based conservation and management strategies tailored to the unique tropical montane ecosystems of the Western Ghats.

5.2 | METHODS

General fruiting patterns

To monitor phenology and quantify fruit biomass from May 2019 to May 2022, a phenological survey was conducted in Eravikulam National Park (ENP). A total of 105 woody species were identified, and trees with clearly visible canopies were selected for regular monitoring. Each tree was tagged with a unique aluminum label, and its girth at breast height (GBH) was measured at 1.3 m above ground. These measurements were later converted to diameter at breast height (DBH) for analysis.

Reproductive phenology (fruiting) was assessed monthly. Observers recorded fruit type, dispersal mode, and evidence of fruit predation based on field signs and previously established trait categories (see Chapter 3). Climate data (temperature, rainfall) were obtained from Kerala Forest Department weather stations within ENP. Seasonal classification followed regional rainfall patterns: dry season (December–April), first wet season (May–August), and second wet season (September–November). Fruiting data were visualized using a phenology calendar across species and months. While all trees ≥ 10 cm DBH were included, variation in reproductive output across size classes was also noted, and larger individuals were prioritized for biomass estimation.

Fruit biomass estimation

Estimates of fruit biomass in the Shola forests of Eravikulam National Park were obtained by sampling fallen fruits at periodic intervals across a defined area. Twenty-five plots, each measuring 10 m \times 10 m, were established on the forest floor, covering an overall area of 0.25 ha. Plot dimensions were adjusted for slope, and multiple smaller plots were utilized to capture a broader range of habitats within the Shola forest than a single large plot. All stems with a diameter at breast height (DBH) of ≥ 10 cm were identified. To record fruiting events nightly, five individuals of each species were selected, following the methodology described by Wheelwright (1988). Peak fruiting values were determined based on the month in which each species produced the highest number of fruits. Ripe fruits on trees or freshly fallen fruits were collected and weighed to the nearest 0.01 g, and fruit biomass production per plot (kg/ha/y) was calculated by multiplying the number of

fruits by the mean fruit weight and dividing by the sampled area, with results extrapolated to a kg/ha basis. During each sampling period, all fruits that fell within the plots, whether consumed or not, were collected, sorted by species, and counted. Ripeness was assessed based on changes in fruit color, size, softness, and appearance of dehiscence lines. The fruits were subsequently returned to the forest away from the plots, whereas a few unidentified fruits were preserved in 70% alcohol for later identification. Fruiting was measured in terms of the number of species bearing fruits each month and the fruit mass per month.

Evaluation of nutrient properties

Proximate analysis

The methods recommended by the Association of Official Analytical Chemists (AOAC) were used to determine moisture, total ash, and crude fiber (AOAC 2005).

Determination of Moisture

The moisture content of the dried fruits of 1 g was determined using the oven-drying method (AOAC, 2005). All measurements were performed in triplicates.

$$\begin{aligned} \text{Moisture Content (\%)} \\ = \frac{\text{Initial weight of sample} - \text{Final weight of sample}}{\text{Initial weight of sample}} \times 100 \end{aligned}$$

Determination of Total Ash

The total ash content of the samples was determined using a muffle furnace (AOAC, 2005). The Dried 1 g fruit sample was carbonized on an oxidizing flame until no fumes were released. It was then ignited at 540 °C in a muffle furnace to burn off all the organic matter. The experiment was repeated thrice. Total ash (%) was calculated as,

$$\text{Total ash (\%)} = \frac{\text{Weight of Ash}}{\text{Weight of Sample}} \times 100$$

Determination of crude Fiber

The fiber content of the dried fruit sample was estimated using the acid-alkali method (Chopra and Kanwar, 1976) with 1.25% H₂SO₄ (prepared by diluting 7.2 mL of 94% conc. Acid of specific gravity 1.835 g mL⁻¹/ 1,000 mL distilled water), and 1.25% NaOH (12.5 g/ 1,000 mL distilled water) solutions. The crude fiber content of the sample was

calculated from the weight loss on ignition and was expressed as a percentage of the fresh weight. Dried fruit samples (1 g) were placed into a 500 ml conical flask, and 200 mL of 1.25% H₂SO₄ was added. The contents were boiled for 30 min, cooled, and filtered through an ashless filter paper. The residue was washed three times with 50 mL aliquots of boiling water. The washed residue was returned to the original conical flask and further digested with 200 mL 1.25% NaOH for 30 min. The digest was then filtered to obtain the residue. This was washed three times with 50 mL aliquots of boiling water, and finally with 25 mL ethanol. The obtained residue was dried to a constant weight in an oven at 130 °C and cooled in a desiccator. The ashless filter paper containing the residue was placed in a pre-weighed crucible, ashed at 550 °C for 6 h, cooled in a desiccator, and reweighed. The experiment was repeated three times, and the crude fiber content was expressed as the percentage loss in weight on ignition.

Determination of Carbohydrate

The dried fruit sample containing carbohydrates was estimated using anthrone reagent, and the absorbance was read at 630 nm against D-glucose as a standard (Dreywood, 1946).

Determination of Crude Protein

The crude protein content of the samples was determined using the Bradford assay. One gram of dried sample was weighed and ground with 1 mL of distilled water using a motor and pestle. The contents were transferred into an Eppendorf tube. All procedures were performed under ice-cold conditions. The samples were then centrifuged at 6500 rpm for 15 min at 40 C. The experiment was performed according to modified Lowry's method by using a DC protein assay kit (Bio-Rad, Hercules, California, USA). The supernatant was used as the test solution, and bovine serum albumin (BSA, 1 mg/ml) was used as a standard. The absorbance was measured at a wavelength of 750 nm (Bradford, 1976). All measurements were recorded in triplicates.

Determination of Crude Fat

The crude fat content of the dried fruit samples was estimated by the fat extraction method Soxhlet apparatus using SOCS –PLUS apparatus (AOAC, 2005) to remove the ether soluble component present in it. Two grams of sample was weighed in a thimble and total fat was extracted with 75 mL diethyl ether at 45.6oC for 120 min. The extracted material

was dried to constant weight in an oven at 70 °C. The experiment was conducted in triplicate. The percentage of crude fat was calculated as,

$$\text{Crude fat (\%)} = \frac{\text{Weight of ether extract}}{\text{Weight of sample}} \times 100$$

Determination of vitamin C

The vitamin C content of the samples were estimated using the AOAC method (1998). The ascorbic acid content of the sample was calculated from the titer value and expressed as mg 100 g/L of the sample.

Determination of total energy

The total energy contained in each sample was calculated using the formula

$$\begin{aligned} \text{Energy(Kcal)} \\ &= 4 \times (\text{Protiens and carbihydrates mass in grams}) \\ &+ 9 \times \text{mass of fat in grams} \end{aligned}$$

Microwave digestion

Six dried fruit samples (0.250 g) were accurately weighed and transferred to a digestion vessel. PerkinElmer Titan MPSTM System with Standard 75 mL digestion vessels was used for the decomposition of the samples. The reagents, 8 mL of HNO₃ (70%), and 2 mL of H₂O₂ (30%) were added slowly to the digestion vessel, and the sample was rinsed to the bottom of the vessel. The system temperature program is presented in Table 1.

Table 5.1 Temperature program for Microwave digestion of fruit sample

Step	Target Temperature (°C)	Pressure Limit (bar)	Ramp Time (min)	Hold Time (min)	Power (%)
1	160	30	5	5	90
2	190	30	3	30	100
3	50	30	1	15	0

Mineral Analysis

The minerals present in the dried powdered fruit were analyzed using inductively coupled plasma-optical emission spectrometry (ICP-OES) (Bakircioglu et al., 2011). The mineral elements such as Calcium (Ca), Cadmium (Cd), Chromium (Cr), Copper (Cu), Iron (Fe), Magnesium (Mg), manganese (Mn), Lead (Pb), Zinc (Zn), phosphorus (P), Mercury (Hg), Arsenic (As) were analyzed using the Perkin Elmer optima ICP- Optical Emission Spectrometer (Model: Avio 200, serial number: 079518071102) and the ICPOES operating conditions are listed in Table 2.

Table 5.2 ICP-AES Instrumental operating conditions and parameters

SL. No	Metals	Ca, Cd, Cr, Cu, Fe, Mg, Mn, Pb, Zn, P	Hg, As
1.	Spray chamber	Ryton Scott spray chamber	Continuous flow hydride generator
2.	ICP RF Power	1500 W	1450 W
3.	Sample Injector	Ceramic injector	Ceramic injector
4.	Plasma Gas Flow	10 L/ min	17 L/ min
5.	Auxiliary Gas Flow	0.2 L/ min	0.2 L/ min
6.	Nebulizer Argon Flow	0.75 L/ min	0.50 L/ min
7.	Sample uptake Rate	1 mL/ min	1 mL/ min
8.	Auto integration	2/20 seconds	2/20 seconds
9.	Data Processing Mode	Axial	Axial
10.	Read Delay	30 seconds	30 seconds
11.	Replicate	2	2

Data analysis

One-way ANOVA was conducted to assess the statistical significance of the differences in fruit biomass and species abundance between different years (2019, 2020, 2021, and 2022) and across the distinct seasons observed within each year. Interaction analysis was performed to examine the combined effects of the year and season on fruit biomass. Pearson's correlation analysis was employed to explore the relationships between the number of fruiting species, total fruit biomass, and various climatic variables, including monthly rainfall and temperature (maximum, minimum, and mean).

5.3 | RESULTS

Among the 105 fruit species sampled, 76% were identified as fleshy, 22% as dry, 1% as dry arils, and 1% as fleshy arils. Drupes were found to be the predominant fruit type, followed by berries. Fifty-four percent of the fruits were dispersed by birds, whereas 14% were dispersed by animals (see Chapter 3).



Figure 5.1 Fruits produced in *Nothapodytes nimmoniana* (J.Graham) Mabb.

Between May 2019 and May 2022, 105 fruiting tree species were recorded. Fruiting activity was observed throughout the year, and at least five fruit-bearing species were recorded each month. A notable decline in total fruit biomass production in the Shola forests was indicated by the analysis, with a decrease from 443.95 kg/ha/y \pm 21.01 in 2019 to 320.69 kg/ha/y \pm 16.43 in 2021, reflecting a significant reduction over the three years (Fig. 2). This decline was evident in both the seed and pulp biomass components. Seeds accounted for 34.6% of the total biomass. The total seed biomass decreased from 151.99 kg/ha/y \pm 9.55 in 2019 to 109.63 kg/ha/y \pm 7.27 in 2021, indicating a significant drop in seed production. Similarly, total pulp biomass fell from 291.96 kg/ha/y \pm 13.47 in 2019 to 211.06 kg/ha/y \pm 11.62 in 2021. The major contributors to fruit biomass at Eravikulam were identified as *Garcinia cowa* Roxb. ex Choisy, *Chionanthus mala-elengi* (Dennst.) P.S. Green, and *Daphniphyllum neilgherrense* (Wight) K. Rosenthal. The reductions in

both seed and pulp biomass suggest potential changes in fruit production dynamics or alterations in the ecological conditions affecting Shola forests.

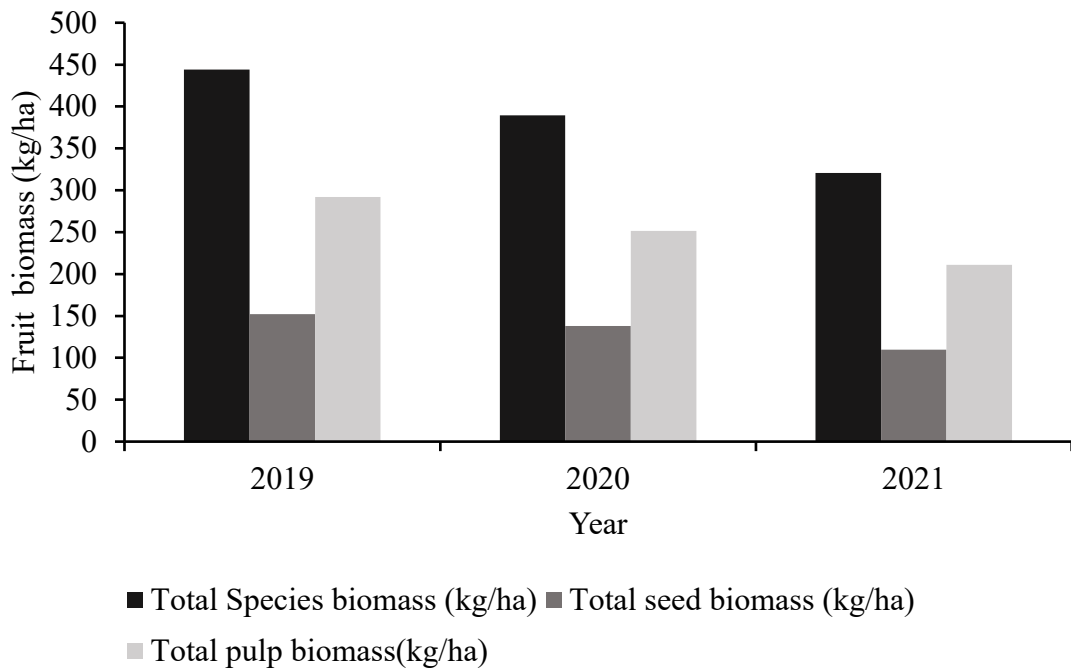


Figure 5.2 Trends in total fruit, seed, and pulp biomass in Shola forests (2019-2021)

General fruiting patterns

The data on monthly total biomass over the three years revealed distinct seasonal variations in biomass production within the study period. The mean biomass over the three years showed a peak in August (71.65 ± 44.16 kg/ha/y) with significant variability, highlighting the high seasonal fluctuation. Fruit production peaked in August, followed by a trough in December (14.37 ± 2.16 kg/ha/y). A continuous decrease in fruit biomass was observed at the beginning and end of the year (Fig. 3). The number of fruiting species varied across months and years, with a peak richness observed in March 2019 and 2020 (29 species). June and July also maintained a high species diversity, with consistent numbers recorded across the years. In contrast, a significant reduction in the number of species was observed in April and May 2020, indicating a possible decline in the fruiting events during these months. Lower species counts were recorded in September and October, aligning with lower biomass levels, while November and December had the fewest fruiting species, reflecting a decrease in both biomass and species richness towards the end of the year. Pearson's correlation analysis revealed a moderately positive

relationship between the number of fruiting species and the amount of fruit biomass ($r = 0.511, p = 0.002$).

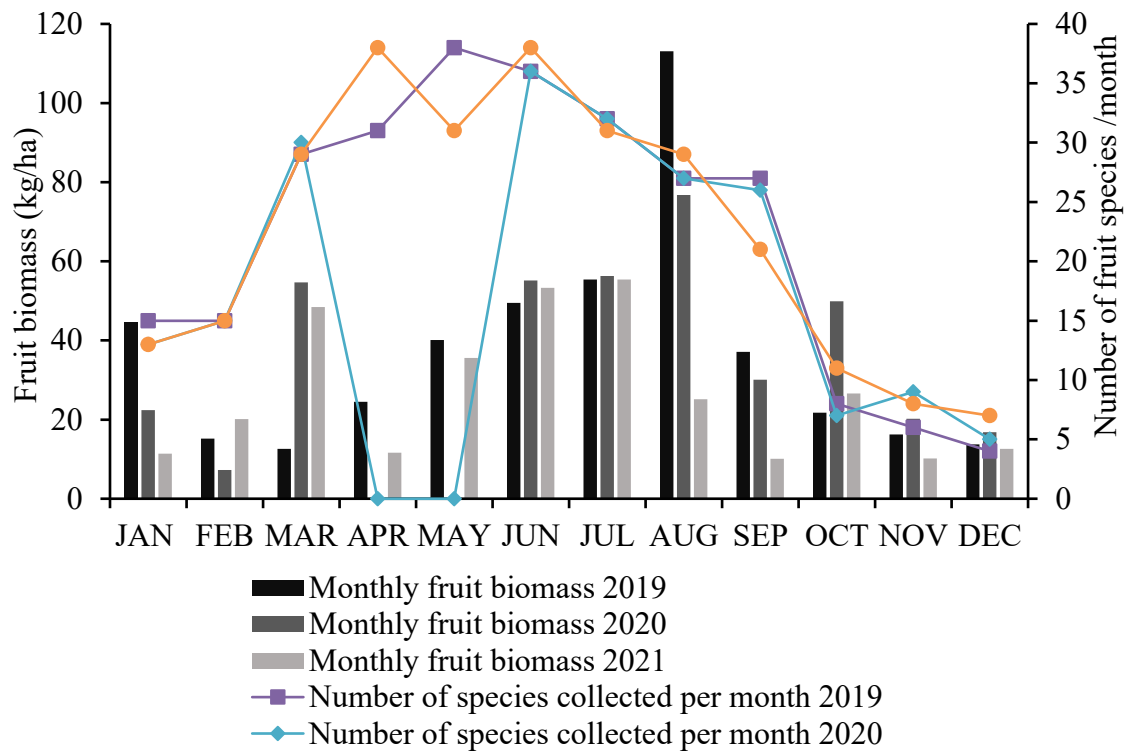


Figure 5.3 Seasonal patterns of fruit biomass and fruiting species diversity in Shola forests: A three-year overview (2019-2021)

The analysis of seasonal patterns in biomass across the Dry, First Wet, and Second Wet seasons revealed significant differences in the biomass levels (Fig. 4). The highest mean biomass was observed during the First Wet season, at 52.78 ± 8.34 kg/ha/y, reflecting peak productivity during this period. In contrast, an intermediate mean biomass of 24.70 ± 5.70 kg/ha/y was recorded during the Second Wet season, while the lowest mean biomass of 16.98 ± 2.75 kg/ha/y was observed during the Dry season, indicating reduced fruit production under drier conditions. Distinct contributions to biomass production were observed during the different seasons ($F = 12.97, p < 0.01$). However, when yearly biomass variations across all seasons were examined, no significant differences were found ($F = 1.631, p = 0.201$), suggesting that the overall biomass did not vary significantly between years. The interaction between year and season was also found to have no statistically significant effect on mean biomass ($F = 0.586, p = 0.673$).

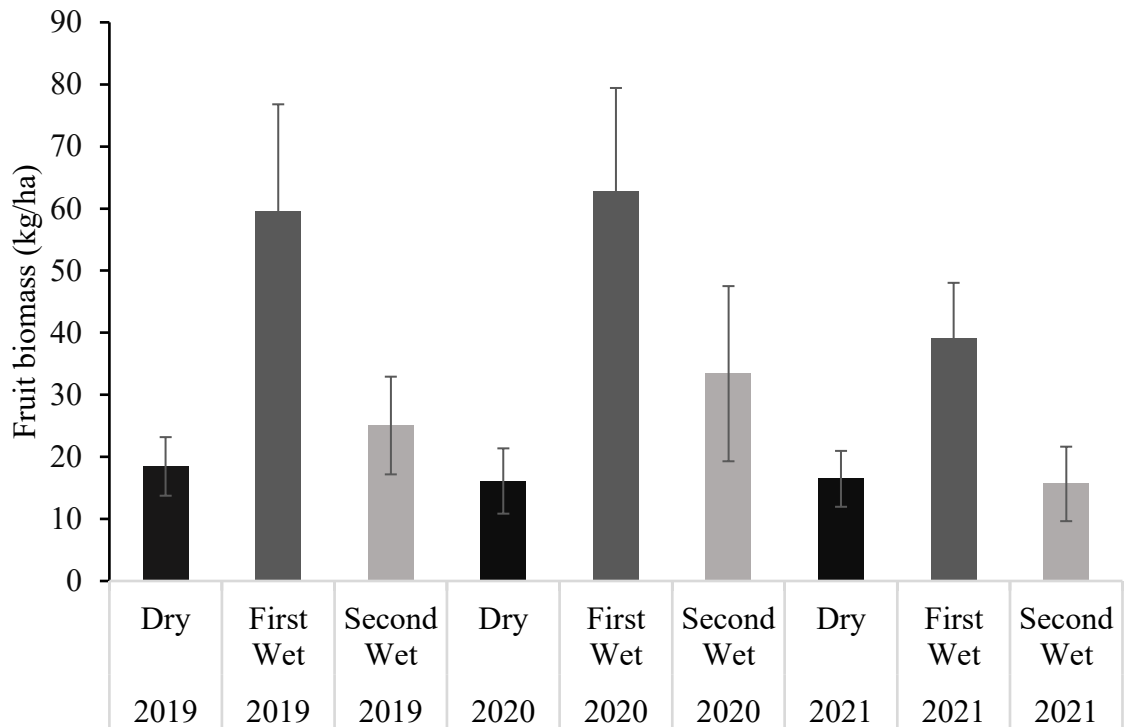


Figure 5.4 Seasonal Variations in Biomass Across Dry and Wet Seasons (2019-2021)

Fruiting patterns under dispersal syndromes

The biomass of fruits belonging to different seed dispersal syndromes contributing to total biomass is presented in Table 3. Bird-dispersed fruits accounted for 59.59% of the total biomass. Ornithochorous fruits consistently represented the highest total biomass, with an average of 229.24 ± 30.97 kg/ha/y, and annual values of 254.01 kg/ha/y in 2019, 248.16 kg/ha/y in 2020, and 185.56 kg/ha/y in 2021, indicating a significant role of bird-dispersed fruits in overall biomass production. Zoochorous fruits contributed an average biomass of 123.99 ± 22.03 kg/ha/y, constituting 32.23% of the total biomass. Mechanically dispersed fruits were recorded at 26.89 ± 3.18 kg/ha/y, contributing 6.99% of the total biomass. Anemochorous fruits were found to have the lowest total biomass among the dispersal syndromes, with an average of 4.08 ± 0.38 kg/ha/y, representing 1.06% of the total biomass and showing a slight increase from 3.71 kg/ha/y in 2019 to 4.60 kg/ha/y in 2021.

Table 5.3 Total biomass of fruits and seeds belonging to different dispersal syndromes in the Shola forest of Eravikulam National Park from 2019-2021

	2019	2020	2021
Total biomass (kg/ha)			
Ornithochorous fruits	254.01	248.16	185.56
Zoochorous fruits	154.87	112.27	104.83
Autochorous fruits	31.37	25.08	24.22
Anemochorous fruits	3.71	3.93	4.60
Seed biomass (kg/ha)			
Ornithochorous fruits	113.22	111.70	81.28
Zoochorous fruits	31.15	19.96	20.87
Autochorous fruits	5.92	4.44	4.85
Anemochorous fruits	1.70	1.77	1.97
Pulp biomass (kg/ha)			
Ornithochorous fruits	140.78	136.47	104.28
Zoochorous fruits	123.72	92.31	83.96
Autochorous fruits	25.45	20.63	19.37
Anemochorous fruits	2.01	2.16	2.63

Bird dispersed fruits

The monthly fruit biomass of each bird species varied substantially across the months. High biomass was observed from June to August, with a peak in August 2019 at 75.02 kg/ha/y, which decreased to 15.37 kg/ha/y in 2021. Lower biomass values were recorded in November and December, with November ranging from 10.53 kg/ha/y in 2019 to 6.63 kg/ha/y in 2021, and December values at 7.95 kg/ha/y in 2019, 10.46 kg/ha/y in 2020, and 7.66 kg/ha/y in 2021 (Fig. 5).

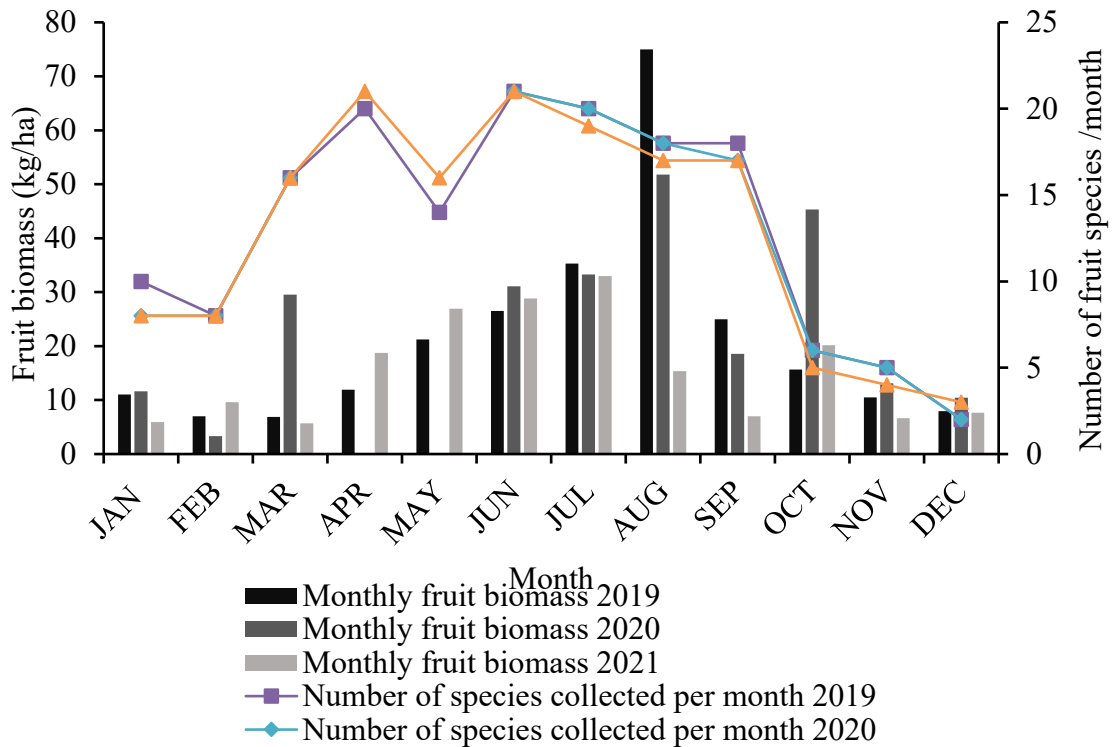


Figure 5.5 Fruit biomass of bird-dispersed species compared with the number of fruit species collected per month over 3 years

A moderate positive correlation was observed between the number of fruiting species and the fruit biomass ($r = 0.469$, $p = 0.005$). The sharp peak in bird fruit biomass, particularly evident in August 2019 (Fig. 5), was primarily attributed to the contributions of *Symplocos cochinchinensis* (Lour.) S.Moore and *Beilschmiedia wightii* (Nees) Benth. ex Hook.f. The ANOVA results revealed significant variations in biomass across different seasons ($F = 12.76$, $p < 0.01$), indicating that seasonal factors substantially affect biomass levels. However, no significant differences were detected in the overall biomass between the years when considering all seasons ($F = 1.634$, $p = 0.21$). The interaction between year and season had no statistically significant effect on mean biomass ($F = 0.952$, $p = 0.450$).

Animal dispersed fruits

The analysis of monthly fruit biomass for animal-dispersed species from 2019 to 2021 revealed significant temporal variability. Notable peaks in fruit biomass were observed in August 2019 (36.83 kg/ha/y) and June 2019 (19.17 kg/ha/y), whereas lower values were recorded in October 2019 (2.89 kg/ha/y). The biomass levels in 2020 were generally lower than those in 2019 and 2021, with relatively higher values observed in March 2020 (19.10 kg/ha/y). In 2021, the highest recorded biomass was in June (20.87 kg/ha/y) and the lowest

was in September (2.52 kg/ha/y). The analysis for April and May 2020 was limited because of the missing data for these months (Fig. 6).

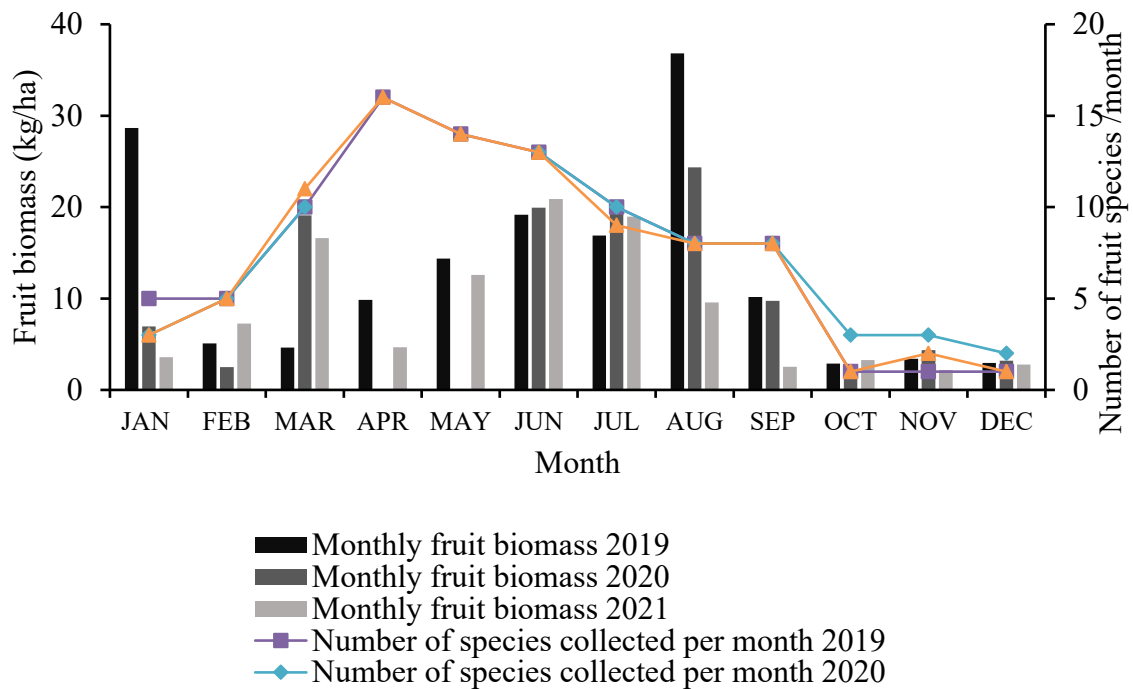


Figure 5.6 Fruit biomass of animal dispersed species compared with the number of fruit species collected per month over 3 years

A statistically significant positive correlation was observed between the number of fruiting species and fruit biomass ($r = 0.644$, $p < 0.01$), indicating that increases in the monthly fruit biomass were associated with increases in the number of fruiting species collected each month. The average biomass across all years was found to be 23.65 ± 6.01 kg/ha/y during the dry season, 58.19 ± 6.44 kg/ha/y during the first wet season, and 13.60 ± 3.14 kg/ha/y during the second wet season, resulting in an overall average of 31.92 ± 4.54 kg/ha/y. ANOVA results showed no significant differences in the overall biomass between years ($F = 1.034$, $p = 0.370$). However, significant variations in biomass were observed between seasons ($F = 13.36$, $p < 0.01$). The interaction between year and season did not significantly affect the biomass levels ($F = 0.252$, $p = 0.906$). These findings suggest that seasonal factors exert a more substantial influence on biomass levels than year-to-year variations.

Mechanically dispersed fruits

The monthly fruit biomass data of mechanically dispersed species for the years 2019, 2020, and 2021 indicated notable fluctuations in biomass levels across the months. The

highest biomass was observed in January 2019, with a value of 5.05 kg/ha/y, whereas the lowest was recorded in August 2021, at 0.22 kg/ha/y (Fig. 7).

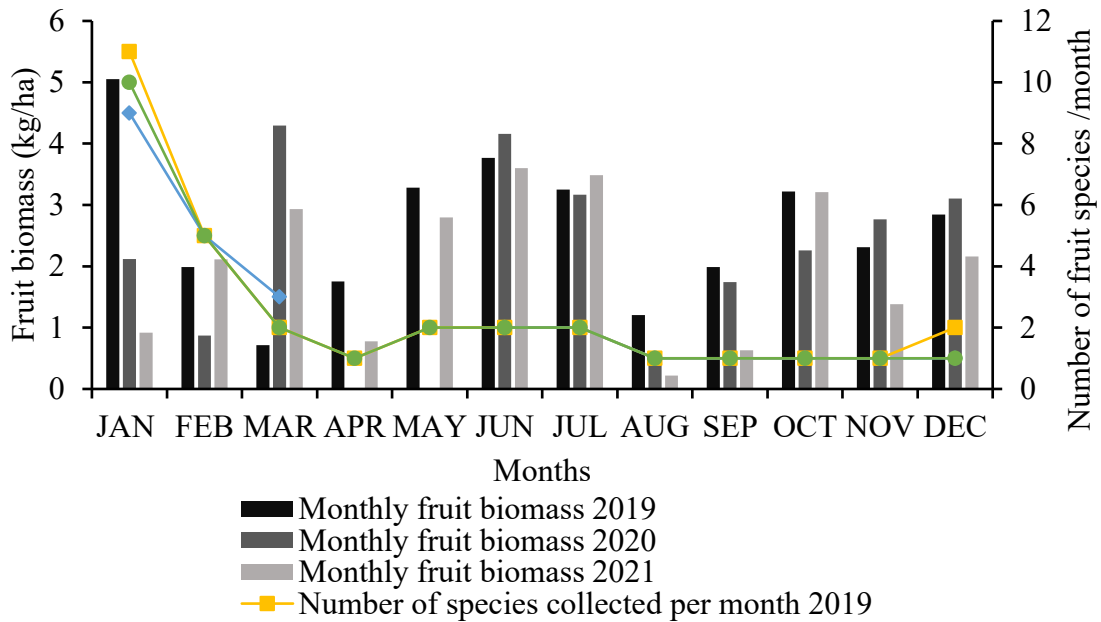


Figure 5.7 Fruit biomass of mechanically dispersed species compared with the number of fruit species collected per month over 3 years

A positive correlation was observed between the monthly fruit biomass and the number of species collected per month, but the correlation was relatively weak ($r = 0.328$, $p = 0.058$). This suggests that, although an association between the two variables may exist, it is not strong enough to be considered statistically significant within this dataset. ANOVA results indicated no significant differences in overall biomass between years ($F = 0.667$, $p = 0.522$) or seasons ($F = 0.438$, $p = 0.650$). Furthermore, the interaction between year and season did not significantly affect the biomass levels ($F = 0.080$, $p = 0.988$).

Wind dispersed fruits

The monthly fruit biomass data for wind-dispersed species available from January to May across the years 2019 to 2021 exhibited notable variations (Fig. 8). The highest biomass values were observed in March 2021, at 1.96 kg/ha/y, while the lowest was recorded in March 2019, with 0.44 kg/ha/y.

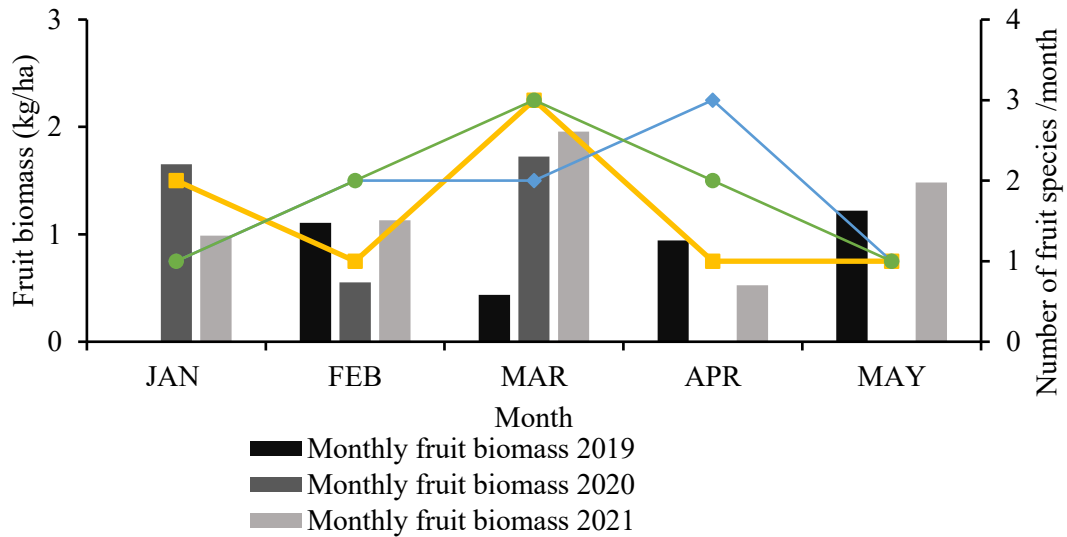


Figure 5.8 Fruit biomass of wind-dispersed species compared with the number of fruit species collected per month over 3 years

A statistically significant positive correlation was found between the number of fruiting species and the fruit biomass ($r = 0.644$, $p < 0.01$). However, the analysis revealed no significant differences in overall biomass across the three years ($F = 0.295$; $p = 0.751$). Because of the absence of wind-dispersed species fruiting during the second wet season, a seasonal comparison of biomass was not feasible.



Figure 5.9 Fruits of (A) *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. (B) *Elaeocarpus munroi* (Wight) Mast. found on the fruit quadrants

Seed production in the Shola forest of Eravikulam National Park

The monthly variation in seed biomass from 2019 to 2021 for different seed types (Ornithochorus, Zoochorous, Autochorous, and Anemochorous) was analyzed (Fig. 10). For Ornithochorus seeds, considerable variability was observed in 2019, with biomass peaking at 33.48 kg/ha/y in August and reaching a low of 3.49 kg/ha/y in December. In 2020, a notable increase in biomass was recorded in June at 23.02 kg/ha/y, while the lowest

value of 1.47 kg/ha/y was noted in February. Data for 2021 revealed the highest biomass in March at 14.67 kg/ha/y and the lowest in September at 2.99 kg/ha/y. For Zoochorous seeds, the highest biomass in 2019 was recorded in August at 9.83 kg/ha/y, and the lowest value was 0.55 kg/ha/y in November. In 2020, biomass peaked in May at 4.39 kg/ha/y, with the lowest recorded in December at 0.48 kg/ha/y. In 2021, the highest biomass was observed in March (3.98 kg/ha/y), whereas the lowest biomass was observed in October (0.42 kg/ha/y).

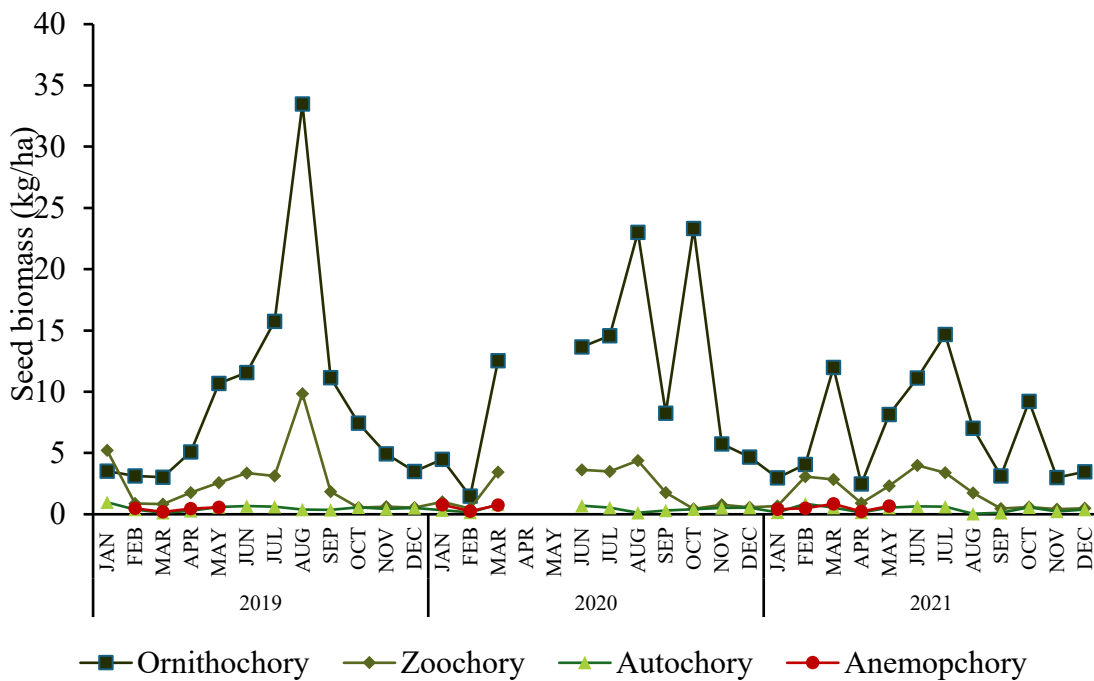


Figure 5.10 Monthly variation of seed biomass from 2019-2020

The Autochorous seed biomass in 2019 was highest in May (0.66 kg/ha/y) and lowest in March (0.12 kg/ha). In 2020, biomass was highest in May (0.71 kg/ha/y) and lowest in April (0.11 kg/ha). In 2021, the highest biomass was recorded in March at 0.63 kg/ha, and the lowest was observed in August at 0.04 kg/ha/y. For Anemochorous seeds, biomass data in 2019 were sparse, with measurements only in February (0.48 kg/ha/y) and March (0.19 kg/ha/y). In 2020, the biomass was recorded in April (0.45 kg/ha/y) and May (0.58 kg/ha/y), with no additional data available. In 2021, the highest biomass was recorded in May (0.85 kg/ha, and the lowest was recorded in September (0.23 kg/ha. The average fruit abundance per fruiting tree was 3.66 kg/tree, indicating the average amount of fruit biomass available per fruiting tree over the three years.

Factors influencing fruiting patterns

The relationships between climatic variables such as rainfall, maximum, minimum, and mean temperature, number of species in fruit, and fruit biomass were recorded. Monthly variations in rainfall and temperature (maximum and minimum) are shown in Figure 11.

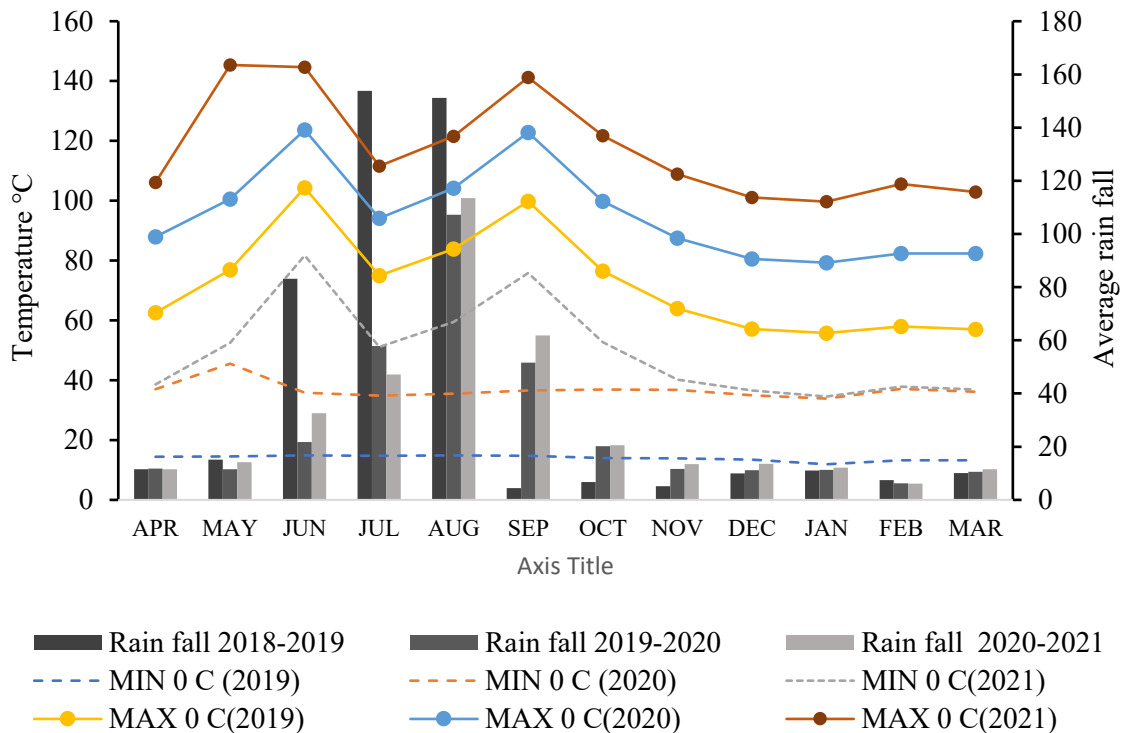


Figure 5.11 Monthly rainfall and temperature recorded from 2019-2020

Species, such as *Garcinia cowa* Roxb. ex Choisy, *Litsea* spp., and *Daphniphyllum neilgherrense* (Wight) K. Rosenthal produce large quantities of fruit in the wet season. During summer, fruits of *Elaeocarpus* spp., *Magnolia nilagirica* (Zenker) Figlar (Zenker) Figlar, *Agrostistachys indica* Dalzell, *Celtis tetrandra* Roxb., and *Elaeocarpus* spp. formed important resources for the faunal community and thus formed a major part of the frugivore diet. Our results indicated that rainfall was significantly positively correlated with the total biomass ($r = 0.518$, $p = 0.002$), seed biomass ($r = 0.534$, $p = 0.001$), and pulp biomass ($r = 0.496$, $p = 0.003$). This is supported by time-lag correlations, which showed the highest correlation ($r = 0.62$, $n = 36$, $P < 0.01$) for a one-month lag between rainfall and fruit production. Species fruits during the first wet period included *Nothapodytes nimmoniana* (J.Graham) Mabb., *Neolitsea cassia* (L.) Kosterm., *Microtropis ramiflora* Wight, and *Litsea wightiana* (Nees) Wall. ex Hook.f. In contrast, the correlation between the total biomass and minimum temperature was significant ($r =$

0.312, $p = 0.042$), whereas the correlation between the total biomass and maximum temperature was not significant ($r = 0.065$, $p = 0.713$). For seed biomass, a significant positive correlation with minimum temperature was observed ($r = 0.345$, $p = 0.045$), whereas no significant correlation was detected with maximum temperature ($r = 0.074$, $p = 0.675$). Pulp biomass demonstrated a significant positive correlation with minimum temperature ($r = 0.286$, $p = 0.001$), but a non-significant correlation with maximum temperature ($r = 0.059$, $p = 0.742$). The correlation with rainfall was significantly positive across all the biomass categories. The major consumers of fruit include the Nilgiri wood pigeon (*Columba elphinstonii*), Palani laughing thrush (*Montecincla fairbanki*), Malabar whistling thrush (*Myophonus horsfieldii*), Malabar giant squirrel (*Ratufa indica*), and Bulbul spp.

Nutritional characteristics of fruits consumed by frugivores

Nutritional analyses were conducted for the species that were widely consumed by frugivores. The results of the nutritional analysis are presented in Table 4. The mineral composition of fruits consumed by frugivores is given in Table 5.

Table 5.4 Proximate composition of *fruits* consumed by frugivores. Individual readings (n = 3) were averaged and presented with \pm SE

Sample	Nutritional Parameters							
	Moisture (%)	Total Ash (%)	Crude Fiber (%)	Carbohydrate (mg/g)	Crude Protein (mg/g)	Crude Fat (%)	Vitamin-C (mg/g)	Energy (kcal)
<i>Garcinia gummi-gutta</i> (L.) N.Robson	12.46 \pm 0.58	7.45 \pm 0.054	7.09 \pm 0.01	143.0 \pm 0.20	62.10 \pm 0.66	15.43 \pm 1.54	0.11	959.27
<i>Litsea wightiana</i> (Nees) Wall. ex Hook.f.	5.433 \pm 0.45	4.88 \pm 0.03	5.33 \pm 0.02	355.5 \pm 0.74	12.83 \pm 0.30	1.06 \pm 0.03	0.05	1482.86
<i>Melicope lunu-ankenda</i> (Gaertn.) T.G.Hartley	24.13 \pm 0.69	2.10 \pm 0.03	4.56 \pm 0.06	822.16 \pm 0.79	43.40 \pm 0.52	12.35 \pm 0.76	0.06	3573.39
<i>Magnolia nilagirica</i> (Zenker) Figlar	16.82 \pm 0.90	3.41 \pm 0.02	6.41 \pm 0.02	260.7 \pm 0.25	27.22 \pm 0.58	0.95 \pm 0.07	0.04	1160.23
<i>Neolitsea scrobiculata</i> Meisn. (Meisn.) Gamble	15.78 \pm 0.31	4.58 \pm 0.02	7.54 \pm 0.02	643.9 \pm 0.59	35.99 \pm 0.62	0.35 \pm 0.05	0.06	2722.71
<i>Ternstroemia gymnanthera</i> (Wight & Arn.) Bedd.	14.88 \pm 0.74	2.04 \pm 0.01	5.34 \pm 0.12	123.03 \pm 1.17	15.49 \pm 0.36	0.70 \pm 0.12	0.11	560.38
<i>Cinnamomum verum</i> J.Presl	15.42 \pm 0.54	8.10 \pm 0.01	7.29 \pm 0.06	223.2 \pm 0.50	42.77 \pm 0.96	0.66 \pm 0.05	0.05	1069.82
<i>Elaeocarpus munroi</i> (Wight) Mast.	18.63 \pm 0.56	7.72 \pm 0.05	5.74 \pm 0.05	57.7 \pm 0.05	189.94 \pm .74	1.06	0.18	1000.1
<i>Litsea scrobiculata</i> Meisn.	7.30 \pm 0.23	2.84 \pm 0.02	6.67 \pm 0.12	133.66 \pm 0.86	183.63 \pm 0.91	1.16 \pm 0.03	0.13	1279.6
<i>Syzygium densiflorum</i> Wall. ex Wight & Arn.	8.78 \pm 0.41	6.88 \pm 0.02	7.57 \pm 0.16	246.6 \pm 0.86	39.18 \pm 0.47	1.20 \pm 0.07	0.09	1153.92
<i>Rhodomyrtus tomentosa</i> (Aiton) Hassk.	10.05 \pm 0.50	7.48 \pm 0.03	7.44 \pm 0.14	27.05 \pm 0.73	46.66 \pm 0.66	1.28 \pm 0.02	0.06	306.36

Table 5.5 Mineral composition in the fruits consumed by frugivores in the Shola forests of Eravikulam National Park

Samples	Ca (mg/kg)	Cd (mg/kg)	Cr (mg/kg)	Cu (mg/kg)	Fe (mg/kg)	Mg (mg/kg)	Mn (mg/kg)	Pb (mg/kg)	Zn (mg/kg)	P (mg/kg)
<i>Garcinia gummi-gutta</i> (L.) N.Robson	335.15	BDL	3.12	2.12	39.01	233.75	2.37	BDL	2.73	289.68
<i>Litsea wightiana</i> (Nees) Wall. ex Hook.f.	1916.87	BDL	2.81	13.43	58.43	373.12	14.68	BDL	19.81	526.09
<i>Melicope lunu-ankenda</i> (Gaertn.) T.G.Hartley	1801.56	BDL	4.06	14.37	46.87	192.81	3.75	BDL	15.17	576.09
<i>Magnolia nilagirica</i> (Zenker) Figlar	254.06	BDL	2.32	1.35	23.71	117.32	2.03	BDL	6.01	240.78
<i>Neolitsea scrobiculata</i> Meisn. (Meisn.) Gamble	1273.90	BDL	2.57	1.50	17.73	321.25	34.62	BDL	4.45	272.65
<i>Ternstroemia gymnanthera</i> (Wight & Arn.) Bedd.	281.87	BDL	2.84	20.51	155.87	5.07	5.07	BDL	16.37	400.62
<i>Cinnamomum verum</i> J.Presl	142.09	BDL	3.06	1.96	19.68	207.5	1.85	BDL	7.75	361.09
<i>Elaeocarpus munroi</i> (Wight) Mast.	85.01	BDL	3.04	1.78	16.96	202.5	2.46	BDL	6.23	381.40
<i>Litsea scrobiculata</i> Meisn.	187.5	BDL	2.84	1.78	16.10	235	2.00	BDL	5.70	382.03
<i>Syzygium densiflorum</i> Wall. ex Wight & Arn.	79.65	BDL	2.98	2.17	18	154.45	1.93	BDL	5.20	332.18
<i>Rhodomyrtus tomentosa</i> (Aiton) Hassk.	82.31	BDL	3.09	1.84	36.39	174.84	2.00	BDL	6.92	369.21

Based on proximate analysis of fruits consumed by frugivores, *Melicope lunu-ankenda* (Gaertn.) T.G.Hartley showed high moisture content (24.13%, SD=1.19, N=3), followed by *Elaeocarpus munroi* (Wight) Mast. (18.63%, SD=0.98, N=3), and *Magnolia nilagirica* (Zenker) Figlar (16.82%, SD=1.56, N=3). A Kruskal-Wallis test revealed significant differences between the moisture content of the 11 samples (H=30.31, p=0.001). Based on the results of the Kruskal-Wallis test, the highest carbohydrate content was found in *Melicope lunu-ankenda* (Gaertn.) T.G.Hartley (H=31.394, p = 0.001). There was a higher protein content in *Elaeocarpus munroi* (Wight) Mast. (189.94, SD=3.11) and *Magnolia nilagirica* (Zenker) Figlar (183.63, SD=1.01). In *Garcinia gummigutta* (L.) N.Robson (15.43, SD=2.68) and *Elaeocarpus munroi* (Wight) Mast. (0.18), fat and vitamin C were higher, respectively. In contrast, ash content was relatively higher in *Cinnamomum verum* J.Presl (8.10, SD= 0.03) and lower in *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. (2.34, SD= 0.02).

The mineral composition of the foods consumed by frugivores showed that *Cinnamomum verum* J.Presl and *Elaeocarpus munroi* (Wight) Mast. had the highest calcium content, whereas *Litsea wightiana* (Nees) Wall. ex Hook.f. and *Elaeocarpus munroi* (Wight) Mast. had the highest chromium content. *Cinnamomum verum* J.Presl contains the highest levels of Mg and Mn among fruits. It is important to note that the amounts of Pb and Cd in all these fruits were very low.

5.4 | DISCUSSION

The Tropical montane forest at Eravikulam National Park produced about 384.69 kg/ha/y of fruits per year which ranged between 320.69 kg/ha/y to 443.95 kg/ha/y. The fruit biomass is similar to that of the moist altitudinal forest of South Eastern Brazil (160- 400 kg/ha/y (Morellato, 1992) and less than the values obtained from the Wet Evergreen forest of Kakkachi (645 kg/ha/y; Ganesh and Davidar 2005), Tropical dry evergreen forest of Sothern India (602-913 kg/ha/yr; Swamynathan and Parthasarathy, 2005), Peru (1990 kg/ha/y; Terborgh, 1983) and lowland forest of Panama (2180 kg/ha/y; Foster, 1982a,b). These values are greater than those of Los Tuxtlas (secondary forest) in Mexico (170 kg/ha/y) and the Japi Mountains (tropical semi-deciduous altitudinal forest) in Brazil (134 kg/ha/y) (Sanchez and Alvarez-Sanchez,1995; Morellato, 1992). Fruit fall studies in tropical and temperate forests by Hanya and Aiba (2010) have shown that the average fruit fall was 454 ± 258 kg/ha/y in tropical forests and 362 ± 352 kg/ha/y in temperate forests.

The abundance of bird and animal dispersal syndromes in fruit biomass also supports the general conclusion that 65% and 90% of woody species in tropical and subtropical Asia (hereafter, the Oriental Region) are dispersed by vertebrates, with birds being dispersed more than mammals (Ganesh and Davidar, 2001; Chen et al., 2004; Datta and Rawat, 2008; Du et al., 2009; Corlett, 2011a; Li et al., 2013; Tadwalkar et al., 2012).

A significant proportion of the biomass in ENP is composed of large fruits, which are either dehiscent or dispersed by large frugivorous birds such as pigeons or mammals. This prominence is likely due to the considerable size of the fruits and their frequent occurrence in samples. Several species, including *Prunus ceylanica* (Wight) Miq., *Chionanthus malaelengi* (Dennst.) P.S. Green and *Garcinia cowa* Roxb. ex Choisy, are found at high densities, fruiting annually, and thus contribute substantially to the overall biomass. Although one might anticipate an association between biomass and abundance, this relationship does not hold, primarily due to the high fruit fall observed in small-sized fruits, such as *Eurya nitida* Korth., *Ixora notoniana* Wall. ex G. Don, and *Litsea floribunda* (Blume) Gamble. Conversely, species with larger fruits contributed significantly to the biomass, despite their lower abundance. Therefore, the importance of certain species in biomass estimation is influenced by a combination of factors, including species density, fruit size, and frequency of fruit fall.

As in most tropical communities, reproductive phenology in tropical montane evergreen forests is intricately linked to ecological factors and climatic conditions and plays a crucial role in ensuring successful plant reproduction. There were important differences in fruiting patterns between seasons in Eravikulam National Park. Our results support the finding that seasonal variations in weather play an important role in shaping the phenology of many plants (Wright and Van Schaik, 1994; Borchert, 1998; Corlett and LaFrankie, 1998). This variation creates a strong tendency for high-fruit production seasons to alternate with low-fruit production seasons. All estimates included the seeds and non-edible parts of the fruit. If we are considering only fresh weight to represent fruit biomass to focus on the availability of resources for frugivorous animals and birds, it is nearly half our estimates (192.34 kg/ha/y) and this can be compared to the lower fruit biomass values found in the literature. Supra-annual fruiting cycles are not uncommon in the tropics, and our study targeted an unusually low year in terms of fruit production (Jordano, 1993; Herrera, 1998).

It was observed that there was no fruiting in the case of *Abarema subcoriacea* (Thwaites) Kosterm. and *Celtis philippensis* Blanco during the study period. This is not uncommon, as there are individuals of many tropical trees that skip fruiting in some years (Hurlbert, 1970). In the case of *Palaquium ravii*, Sasidh. & Vink fruits were present throughout the year, peaking in May-June, which is the pre-monsoon period. *Chukrasia tabularis* A.Juss. was fruited throughout the year. However, in this case, a peak was observed during February- March, which is the dry period.

In the Eravikulam Shola forests, fruiting activity peaked during the wettest periods of the year (June to August), whereas low fruiting periods typically occurred during the late wet and early to mid-dry seasons. After heavy rain, the number of fruiting species decreased, as did total fruit production. This pattern aligns with the findings of other tropical studies (Tutin et al., 1991; Silvius, 2002; Stevenson, 2004). The availability of ripe fruits, as measured by the number of fruiting individuals, species, and fruit mass, was positively correlated with the rainfall. Most fleshy fruits in Eravikulam Shola are produced during the wet season of the year. Fruits ripened during December or January usually wait until April or May, before reliable rain permits germination. Similarly, fleshy fruits were produced during the wettest period of the year in the relatively seasonal forests of eastern Costa Rica (Frankie et al., 1974) and Colombia (Hilty, 1980). The occurrence of peak fruiting during the rainy season is indicative of fruit phenology during the optimal seed germination period, which occurs during prolonged wet periods, as supported by the germination hypothesis (van Schaik et al., 1993). Ripening of fruits close to rainfall can help achieve post-dispersal success (Rathcke and Lacey, 1985), enhance seed dispersal (Prasad and Sharathchandra, 1984), and avoid pathogen infection (Augspurger, 1983). In the tropical montane forests of the upper Nilgiri Mountains of South India, and the tropical dry forest in Mudumalai, South India, germination showed a community-wide peak during the wet season (Mohandas et al., 2016; Murali and Sukumar, 1994). Fruiting peaks during the wet season have also been observed in gallery and montane forests along the Lençóis River, state of Bahia, Brazil (Funch et al., 2002), and in mesophilic semi-deciduous and deciduous forests (Lieberman 1982, Morellato et al., 2000).

Wind-dispersed fruit production has been reported during the dry season in the deciduous forests of western Costa Rica (Frankie et al., 1974), seasonal wet forests of Panama (Foster, 1982), Guyana (Charles-Dominique et al., 1981), and Brazil (Jackson, 1981), which supports our results. In Eravikulam Shola similar pattern was observed, species that are

dispersed by wind, such as *Chukrasia tabularis* A.Juss., *Gordonia obtuse* Wall. ex Wight & Arn., and *Pterocarpus marsupium* Roxb., which fruited mainly during the dry season. Mechanically dispersed fruits dehisce during dry months when relative humidity is low (Murali and Sukumar, 1994).

Both rainfall availability and minimum temperature affected fruit production in the ENP. Fruit production is more influenced by minimum temperature than the absence of rainfall, as indicated by the observation of fruiting throughout the dry season despite low rainfall. This can be explained by the reduced respiration rates and accumulation of biomass in plants as a result of conserving energy resources (Amthor, 1984). The synergistic action of rainfall and minimum temperature can be seen in fruit production in Shola. Sufficient rainfall along with cooler temperatures can provide suitable growth conditions for plants by reducing water stress and guaranteeing sufficient water availability that eventually increases fruit biomass production (Chapin et al., 2011; Sala et al., 2012; Jones, 2013).

The flowering and fruiting patterns of frugivores in ENAP are closely associated with the resource availability for frugivores and pollinators. The availability of edible fruits significantly influences the population dynamics of frugivore communities (Leigh, 1999; Smythe et al., 1982; Wright et al., 1999). Mammal survival and reproduction have been connected to fruit availability and consumption (Eiler et al., 1976; Rogers, 1976; Reynolds-Hogland et al., 2007). These frugivores aid seed dispersal, resulting in changes in plant community structure and dynamics (Wright et al., 2005; Morales et al., 2013). In ENP, 76% of the fruits produce fleshy and edible biomass, which serves as a crucial food resource for frugivores. Several key species, including *Litsea* spp., *Elaeocarpus* spp., *Magnolia nilagirica* (Zenker) Figlar (Zenker) Figlar, and *Glochidion neilgherrense* Wight, are particularly important because they produce fleshy fruits, which are essential for many vertebrate species. Species, such as *Ixora wightiana* Wall. and *Litsea floribunda* (Blume) Gamble, were primarily dispersed by birds and animals during the wet season. In tropical humid environments, zoochoric species tend to produce fleshy fruits most often during the rainy season, which is considered favorable because of the increased activity of animals (Smythe, 1970; Frankie et al., 1974; Howe and Smallwood, 1982). Among the major frugivores in ENP are bulbuls, including Red-whiskered bulbuls (*Pycnonotus jocosus*), Red-vented bulbuls (*Pycnonotus cafer*), Grey-headed bulbuls (*Brachypodius priocephalus*), Yellow-browed bulbuls (*Iole indica*), and Black bulbuls (*Hypsipetes leucocephalus*). Other significant frugivores include Nilgiri wood pigeon (*Columba*

elphinstonii), Palani-laughing thrush (*Montecincla fairbanki*), Barbets, Nilgiri langur (*Semnopithecus johnii*), and Malabar giant squirrel (*Ratufa indica*). Given the critical role of specific fruit species in the diets of particular frugivore species, it may be necessary to monitor these species with one another rather than, conducting broader sampling of floral and faunal communities. Understanding the complexities of this ecosystem requires detailed monitoring of frugivores in the Shola forests of ENP and their associated floral partners, as elaborated in Chapter 4.

Proximate analysis revealed key nutritional differences in fruits consumed by frugivores, which likely influenced their dietary choices. The high moisture content in *Melicope lunu-ankenda* (Gaertn.) T.G.Hartley, *Elaeocarpus munroi* (Wight) Mast., and *Magnolia nilagirica* (Zenker) Figlar may make these fruits valuable hydration sources, particularly during dry periods. The high carbohydrate content in *Melicope lunu-ankenda* (Gaertn.) T.G. Hartley's provides energy, while the high level of protein in *Elaeocarpus munroi* (Wight) Mast. and *Magnolia nilagirica* (Zenker) Figlar supports frugivores with necessary proteins. *Cinnamomum verum* J.Presl, rich in essential minerals, may help fulfil the dietary mineral requirements of frugivores. In Shola forests, these variations demonstrate how the fruit nutrient composition can influence frugivore preferences and drive seed dispersal in Shola forests.

This study established a baseline for understanding fruit production and frugivore dynamics in ecosystems by providing quantitative records of fruit production and details of fruiting phenology. In the Sholas of Eravikulam National Park, our findings revealed that most fleshy fruiting tree species had a regular seasonal reproductive cycle. The timing of fruiting is determined by water-related factors that are important for seed germination during the rainy season. To further validate our findings long-term phenological studies are necessary. Our investigation provides a solid understanding of the intricate ecological interactions regulating reproductive phenology. This knowledge can support the development of management plans to protect the biodiversity and integrity of the Shola forests.

5.5 | IMPLICATIONS FOR CONSERVATION

Critical ecological process such as the production of fruits by the trees supports a diverse range of frugivores, including birds, mammals, and insects. The survival, reproduction, and population dynamics of frugivore community are directly linked to the availability of

food resources (Corlett, 2011). Quantifying fruit biomass can measure the availability of resources. This data can guide conservation strategies aimed at maintaining a healthy ecosystem (Levey, Silva, and Galetti, 2002).

In fragmented landscapes, isolated patches of forests are created as a result of habitat alteration and degradation. Disruption in the natural patterns of fruit production and availability after habitat fragmentation causes declines in frugivore populations and interrupted species interactions (González-Varo et al., 2023). By quantifying fruit biomass in fragmented ecosystems, critical food resources for birds and animals can be identified (Tschardt et al. 2012). These measures are crucial for ensuring the coexistence of frugivores and the plant species they disperse, which play key roles in forest regeneration (McConkey and O’Farrill, 2015).

Understanding the temporal and spatial variations in fruit production patterns can help in the timing and placement of conservation initiatives. Conservation efforts can prioritize the protection of major fruit-producing species during peak fruiting periods, ensuring that frugivores have access to an adequate supply of resources (Corlett, 2011). This information is vital for predicting the impact of changing climate cycles on fruiting patterns, which can help to identify potential risks to biodiversity (Tschardt et al., 2012). Fruit biomass studies support long-term conservation objectives by guiding the creation of sustainable forest management strategies that balance the needs of wildlife with those of local communities (Levey, Silva, and Galetti, 2002).

5.6 | CONCLUSION

The annual fruit biomass in the Shola forests of ENP on average was 384.69 kg/ha/y, with a minimum of 320.69 kg/ha/y to a maximum of 443.95 kg/ha/y during the three-year study period. We observed a significant portion of large fruits in the total fruit biomass. Large fruits were often dispersed by large-bodied frugivorous birds and mammals. Despite their lower abundance, large fruits constitute a larger portion of the overall biomass than smaller fruits, which have higher fall rates.

We observed pronounced variations in fruit production, with peak fruit production occurring during the wettest period of the year. This aligns with the general pattern observed in tropical forests, where climatic factors, such as rainfall and temperature, have a significant impact on fruiting cycles. The fruiting peaks observed during the rainy season in ENP support the germination hypothesis, which suggests that wet periods are associated

with optimal seed germination conditions. Fruit production in ENP is influenced by minimum temperature, which supports the idea that lower temperatures promote biomass accumulation by lowering plant respiration rates.

The frugivore bird and animal populations in Shola depend on the availability of fleshy fruit. The complex association between frugivore diets and fruiting patterns is demonstrated by the frugivore community in the ENP, which includes bulbuls, doves, pigeons, and mammalian seed dispersers. Nutritional studies have emphasized a preliminary understanding of how fruit composition affects frugivore eating choices and seed dispersal. Knowing these nutritional characteristics is important for conservation because it makes it easier to identify the important plant species that maintain frugivore populations.

5.7 | RECOMMENDATIONS

1. Identification and monitoring of key fruit-producing species that play significant roles in supporting frugivore populations. Protect these species, especially during peak fruiting periods, to ensure that frugivores have access to essential food resources. This approach will contribute to the conservation of both plant and animal species that depend on these fruits.
2. Incorporate climate change projections into conservation planning to anticipate potential impacts on fruiting patterns and biodiversity. Given the observed relationships between rainfall, temperature, and fruit biomass, it is crucial to develop adaptive management strategies to address the effects of changing climatic conditions on fruit production and frugivore populations.
3. Advocate and implement sustainable forest management practices that balance the needs of wildlife and local communities. Effective forest management should consider the ecological importance of fruit biomass and strive to maintain healthy forest ecosystems that support both biodiversity and socioeconomic value.
4. Support ongoing research and monitoring efforts to track changes in fruit biomass, frugivore populations, and ecosystem health. Regular data collection will provide valuable insights into refining conservation strategies and adapting to emerging challenges. Continued research is essential to understand the dynamics of fruiting systems and their role in forest conservation.

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Appendix 3. Fruiting phenology calendar of 105 tree species from May 2019– May 2022.

Family	Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Rubiaceae	<i>Ixora wightiana</i>												
fabaceae/Leguminosae	<i>Abarema subcoriacea</i>												
Lauracea	<i>Actinodaphne bourdellonii</i>												
Lauracea	<i>Actinodaphne bourneae</i>												
Lauracea	<i>Actinodaphne salicina</i>												
Meliaceae	<i>Aglaiia apiocarpa</i>												
Euphorbiaceae	<i>Agrostistachys indica</i>												
Euphorbiaceae	<i>Antidesma montanum</i>												
Meliaceae	<i>Aphanamixis polystachya</i>												
Icacinaceae	<i>Apodytes beddomi</i>												
Lauraceae	<i>Apollonias arnotti</i>												
Euphorbiaceae	<i>Aporosa fusiformis</i>												
Myrsinaceae	<i>Ardisia pauciflora</i>												
Myrsinaceae	<i>Ardisia rhomboidea</i>												
Lauraceae	<i>Beilschmiedia wightii</i>												
Flacourtiaceae	<i>Casearia thwaitesii</i>												
Celastraceae	<i>Cassine paniculata</i>												
Ulmaceae	<i>Celtis philippensis</i>												
Ulmaceae	<i>Celtis tetrandra</i>												
Oleaceae	<i>Chionanthus mala elangi</i>												
Oleaceae	<i>Chionanthus ramiflorus</i>												
Meliaceae	<i>Chukrasia tabularis</i>												
Lauraceae	<i>Cinnamomum macrocarpum</i>												
Lauraceae	<i>Cinnamomum sulphuratum</i>												
Lauraceae	<i>Cinnamomum wightii</i>												
Menispermaceae	<i>Cocculus laurifolius</i>												
Lauraceae	<i>Cryptocarya beddomei</i>												

Family	Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Lauraceae	<i>Cryptocarya lawsonii</i>												
Lauraceae	<i>Cryptocarya neilgherrensis</i>												
Bombaceae	<i>Cullenia excelsa</i>												
Daphniphyllaceae	<i>Daphniphyllum neilgherrense</i>												
Sapindaceae	<i>Dodonaea viscosa</i>												
Elaeocarpaceae	<i>Elaeocarpus munroi (Wight) Mast.</i>												
Elaeocarpaceae	<i>Elaeocarpus recurvatus</i>												
Elaeocarpaceae	<i>Elaeocarpus tuberculatus</i>												
Celastraceae	<i>Euonymus crenulatus</i>												
Theaceae	<i>Eurya japonica</i>												
Pentaphylacaceae	<i>Eurya nitida</i>												
Loganiaceae	<i>Fagraea ceilanica</i>												
Clusiaceae/ Guttiferae	<i>Garcinia cowa</i>												
Euphorbiaceae	<i>Glochidion candolleanum</i>												
Euphorbiaceae	<i>Glochidion ellipticum</i>												
Euphorbiaceae	<i>Glochidion neilgherrense</i>												
thymeleaceae	<i>Gnidia glauca</i>												
Icacinaceae	<i>Gomphandra coriacea</i>												
Theaceae	<i>Gordonia obtusa</i>												
Flacourtiaceae	<i>Hydnocarpus alpina</i>												
Aquifoliaceae	<i>Ilex denticulata</i>												
Aquifoliaceae	<i>Ilex gardneriana</i>												
Aquifoliaceae	<i>Ilex walkeri</i>												
Aquifoliaceae	<i>Ilex wightiana</i>												
Sapotaceae	<i>Isonandra candolleana</i>												
Rubiaceae	<i>Ixora notoniana</i>												
Lauraceae	<i>Litsea bourdillonii</i>												
Lauraceae	<i>Litsea coreacea</i>												
Lauraceae	<i>Litsea floribunda</i>												

Family	Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Lauraceae	<i>Litsea wightiana</i>												
Euphorbiaceae	<i>Macaranga peltata</i>												
Magnoliaceae	<i>Magnolia nilagirica (Zenker) Figlar</i>												
Berberidaceae	<i>Mahonia leschenaultii</i>												
Euphorbiaceae	<i>Mallotus tetracoccus</i>												
Cornaceae	<i>Mastixia arborea</i>												
Rutaceae	<i>Melicope lunu-ankenda</i>												
Sabiaceae	<i>Meliosma pinnata</i>												
Sabiaceae	<i>Meliosma simplicifolia</i>												
Clusiaceae/ Guttiferae	<i>Mesua ferrea</i>												
Celastraceae	<i>Microtropis ovalifolia</i>												
Celastraceae	<i>Microtropis ramiflora</i>												
Lauraceae	<i>Neolitsea cassia</i>												
Lauraceae	<i>Neolitsea fischeri</i>												
Lauraceae	<i>Neolitsea scrobiculata Meisn. (Meisn.) Gamble</i>												
Icacinaceae	<i>Nothapodytes nimmoniana</i>												
Oleaceae	<i>Olea paniculata</i>												
Sapotaceae	<i>Palaquim ellipticum</i>												
Sapotaceae	<i>Palaquium ravii</i>												
Lauraceae	<i>Persea macrantha</i>												
Lauraceae	<i>Phoebe wightii</i>												
Rosaceae	<i>Photinia integrifolia</i>												
Rosaceae	<i>Photinia notoniana</i>												
Fabaceae/ Leguminosae	<i>Pithecellobium subcoriaceum</i>												
Pittosporaceae	<i>Pittosporum tetraspermum</i>												
Araliaceae	<i>Polyscias acuminata</i>												
Rosaceae	<i>Prunus ceylanica</i>												

Family	Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Fabaceae/Leguminosae	<i>Pterocarpus marsupium</i>												
Rosaceae	<i>Rapanea capitellata</i>												
Myrsinaceae	<i>Rapanea thwaitesii</i>												
Ericaceae	<i>Rhododendron nilagiricum</i>												
Araliaceae	<i>Schefflera racemosa</i>												
Symplocaceae	<i>Symplocos cochinchinensis</i>												
Symplocaceae	<i>Symplocos foliosa</i>												
Symplocaceae	<i>Symplocos obtusa</i>												
Symplocaceae	<i>Symplocos spicata</i>												
Symplocaceae	<i>Symplocos pendula</i>												
Myrtaceae	<i>Syzygium densiflorum</i>												
Myrtaceae	<i>Syzygium gardneri</i>												
Myrtaceae	<i>Syzygium grande</i>												
Myrtaceae	<i>Syzygium hemisphericum</i>												
Pentaphylacaceae	<i>Ternstroemia gymnanthera</i>												
Theaceae	<i>Ternstroemia japonica</i>												
Meliaceae	<i>Trichilia connaroides</i>												
Staphyleaceae	<i>Turpinia cochinchinensis</i>												
Vacciniaceae	<i>Vaccinium leschenaultiana</i>												
Vacciniaceae	<i>Vaccinium neilgherrense</i>												
Asteraceae/ Compositae	<i>Vernonia monosi</i>												
Caprifoliaceae	<i>Viburnum coriaceum</i>												

Role of abiotic factors in frugivory, seed dispersal, and co-evolutionary dynamics in Shola ecosystems

ABSTRACT

Located at high elevations in the Western Ghats, the Shola forests exhibit an interesting interplay between fruit characteristics, frugivores, and abiotic factors, such as rainfall, temperature, and altitude. This study examined the relationship between frugivore assemblages, environmental conditions, and fruit morphological traits in the Shola forests of Eravikulam National Park, with a focus on ecosystem services such as seed dispersal. Forty four Shola patches of varying sizes at different altitudinal ranges (1690-2024) were examined to understand the relationships between abiotic factors such as temperature, rainfall, altitude, and elevation with frugivore density, body sizes and fruit traits. Our results indicate that Shola forest patches at lower elevations harbor a high density of frugivores and that frugivore density decreases with increasing altitude. The decline in frugivore density was attributed to harsh climatic conditions, such as frost, low soil nutrition, and heavy wind at high-elevation Shola patches. Higher elevations were predominated by smaller fruit consumers such as Nilgiri flowerpecker, while large-bodied fruit consumers such as Nilgiri langur, jackal, and civets, which are abundant at lower elevations. Frugivore gape width, body mass, and fruit size were associated, suggesting the consumption of larger fruits and seeds by large frugivores, which eventually helps in the dispersal of large seeds to longer distances in lower elevational Shola forests. It was discovered that abiotic variables such as rainfall and temperature had a substantial effect on frugivore abundance. Increased fruit availability during months of heavy rainfall may be related to the abundance of frugivores. This study also highlighted how fruit and seed morphologies adapt to different dispersal mechanisms. Higher elevations were associated with smaller and lighter fruits and seeds, indicating a substantial negative association between altitude and fruit and seed sizes. This study suggests that, as altitude

increases, plants may produce smaller fruits to suit the feeding preferences of smaller-bodied frugivores. Patch size and altitude modify dispersal syndromes; at higher elevations, wind-dispersed species were more prevalent, whereas self-dispersed species predominate in smaller patches. These findings advance our knowledge of seed dispersal dynamics in tropical montane forests by highlighting the intricate relationships between frugivores, plant characteristics, and environmental gradients. This study is one of the first to conduct a detailed examination of the responses of frugivores and plant morphology to abiotic variables in the Shola ecosystem, thereby providing vital data for decision-making in Shola restoration and conservation initiatives.

6.1 | INTRODUCTION

Seed dispersal is an ecosystem process that determines floral diversity and forest regeneration in the tropics, especially in tropical montane forests, which are high-elevation forests. These ecosystems are characterized by the naturally fragmented structure of forests and the strong influence of abiotic factors such as elevation, temperature, and rainfall (van Schaik et al., 1993; Ghazoul and Sheil, 2010). In addition, biotic factors, such as frugivore abundance, also influence seed dispersal. These biotic and abiotic variables may change depending on the topography (McCain, 2009). In tropical montane forests, elevation often impacts the climatic conditions, which in turn influence the frugivore populations and fruit availability (McCain, 2009). Temperature tends to decrease and rainfall patterns shift with elevational gradients, which affects fruit production and availability to frugivores, eventually affecting seed dispersal (Ghazoul and Sheil, 2010). While smaller forest patches restrict frugivore availability and seed dispersal, larger forest patches often support more frugivores and increase the probability of successful seed dispersal (Lehouck et al., 2009). Fruit traits and frugivores interact with each other and play a major role in seed dispersal efficiency.

The consumption of fruits by frugivores is determined by fruit and seed traits, such as size and weight (Jordano, 2000). Frugivores that are larger in size, such as primates, tend to disperse large fruits and seeds, but smaller frugivores, such as flowerpeckers, usually disperse smaller seeds (Wheelwright, 1985). In Shola forests, this distinction may enhance the coexistence of fruits with varying attributes, which may improve biodiversity in the ecosystem (Bollen et al., 2004). These morphological traits are adaptations of plants to enhance the

successful dispersal of seeds to suitable microhabitats by attracting frugivores and seed dispersers. (Jordano, 2000; Herrera, 2002). Therefore, it is imperative to investigate how plant traits and frugivores function together to promote seed dispersal.

In montane forests of the Western Ghats such as Shola, climatic conditions and vegetation change along the elevation. Along with elevation Shola patches also change in size and structure, which creates a distinct microhabitat for plants and animals. This could include faunal and floral species of conservation importance. The fragmented nature of Shola, along with the isolation of these habitats with mountain tops, makes the seed dispersal process extremely challenging. Along with these the heavy wind and frequent frost make the germination and survivability of seeds difficult. Therefore, studies on the combined functions of biotic and abiotic factors are significant. Previous studies have mainly focused on large continuous forests or lowland forests, leaving a knowledge gap on how seed dispersal functions in small, fragmented forest patches, as seen in ecosystems such as Shola. Studies addressing the combined effects of abiotic and biotic factors on seed dispersal remain limited in montane regions, despite their recognized ecological and conservation value.

In light of ongoing climate change and habitat alternation in the Western Ghats, which is home to rich diversity and endemism, knowledge of seed dispersal processes and underlying mechanisms is extremely important (Pascal, 1988; Robin and Nandini, 2012). Therefore, this study investigated how the elevation and forest patch size influence the frugivore diversity, availability and morphological characteristics. We also explored how fruit characteristics, such as size and weight, vary with altitude. Based on these baseline data, we investigated how these factors work together to enhance the dispersal process, thus contributing to an improved understanding of plant-frugivore coevolution in Shola. As these studies can lay the foundation for the ecological processes that maintain biodiversity in fragmented landscapes, the findings of this study may provide significant information for forest management and conservation initiatives.

6.2 | METHODS

44 forest patches within the Shola grassland ecosystem, located between latitudes of 10°08' N and longitudes of 77°03' E, were studied to investigate the role of abiotic factors (Fig. 1). Data were collected from the Shola fragments at elevations between May 2019 and May 2022.

The altitudinal range selected for this study varied from 1650 to 2100 meters above sea level and patch sizes ranged from 0.05 to 1.26 ha. Following the classification of Mohandass and Davidar (2010), Shola patches were categorized into three size classes: small (<0.5 ha), medium (≥ 0.5 ha to <1 ha), and large (>1 ha).

Temperature and rainfall data were recorded for each forest patch during the study period (May 2019–May 2022) using data loggers placed at different locations by the Kerala Forest Department. These measurements were recorded consistently throughout the study period to capture seasonal and spatial variability across different abiotic variables.

Dispersal spectra and fruit morphology

In each forest patch, the dispersal spectra of all the fruiting tree species were recorded. Each species was classified based on its primary dispersal syndrome (such as zoochory, anemochory). Dispersal spectra were determined by assessing the proportion of each dispersal syndrome across different patches. Morphological characteristics of the fruits produced by the surveyed species were also recorded. Key fruit traits, including size, shape, color, and diaspore type, were documented to analyze their potential role in attracting frugivores and influencing dispersal success. Diaspore types were classified based on the standard morphological criteria (Chapter 3).

Frugivore assemblages and morphological data

Frugivore assemblages were surveyed in each patch to identify species that contributed to seed dispersal. Frugivore abundance was calculated as the number of individuals per hectare (individuals/ha) using line transects across patches. Species presence and counts were systematically recorded to determine the frugivore diversity and population density in each forest patch. Morphological data, including body mass and gape width, were collected for each frugivore species following the methodology described by Kitamura et al. (2002).

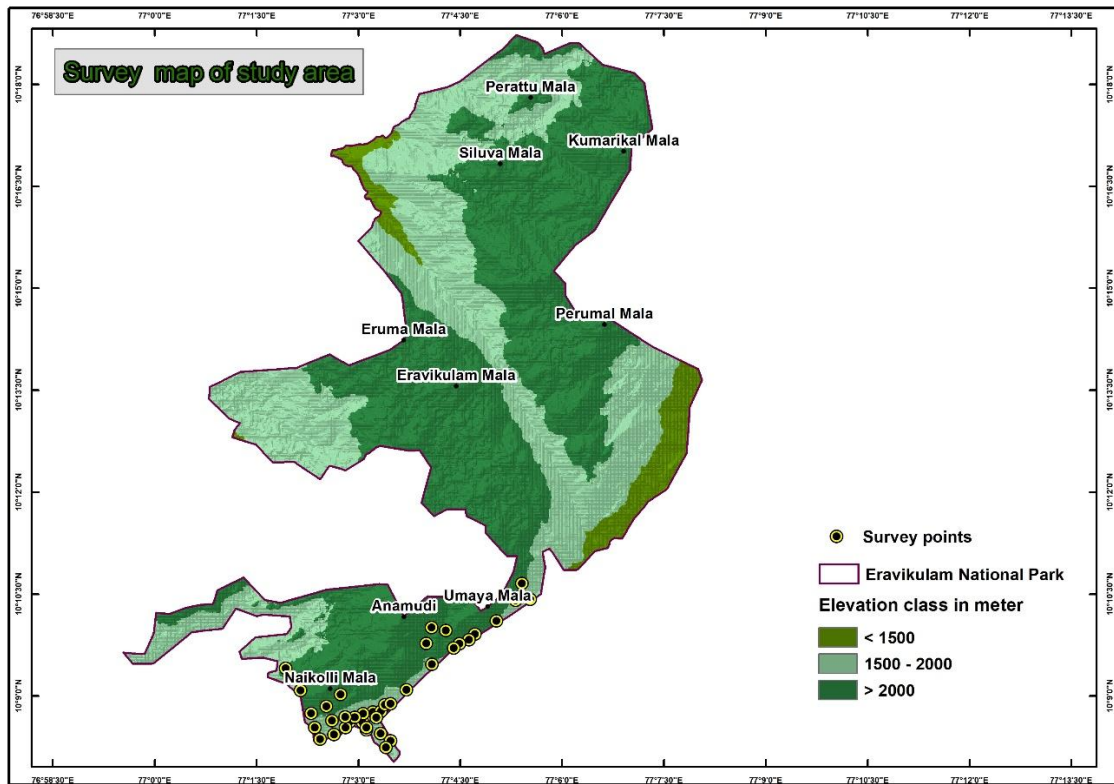


Figure 6.1 Map of the study area

Data analysis

Pearson’s correlation coefficients were calculated to assess the relationships between altitude, patch size, species richness, stem density, and the proportion of different dispersal syndromes (anemochory, autochory, zoochory, and ornithochory). Descriptive statistics were used to summarize the characteristics of the Shola patches, including the range of patch size, species number, and stem density. Simple regression analysis was applied to examine the relationship between fruit and seed traits, and the factors influencing altitude and patch size. Intercorrelations among the different dispersal modes were analyzed to identify the functional distinctions between them. This involved calculating the correlation coefficients between the proportions of anemochorous, autochorous, zoochorous, and ornithochorous species, to explore their relationships and potential competitive interactions.

Pearson’s correlation coefficients were calculated to assess the relationship between frugivore abundance and environmental variables, including altitude, rainfall, and temperature.

Additional correlation analyses were performed to explore the relationships between frugivore body mass and morphological traits (gape width, fruit size, and seed size). Linear regression analysis was used to model the potential relationship between frugivore abundance and environmental factors.

6.3 | RESULTS

At the Eravikulam National Park, the lowermost boundary studied was 1690m. The woody species observed here include *Hydnocarpus alpinus* Wight, *Symplocos foliosa* Wight, *Elaeocarpus tuberculatus* Roxb., *Syzygium gardneri* Thwaites and *Palaquium ellipticum* (Dalzell) Baill. From 1800 m onwards, the forest is almost undisturbed with large trees (mainly *Elaeocarpus* sp., *Litsea* spp., and *Syzygium* spp.) that often grow 25-30 m tall. At 2000 m species such as *Vaccinium leschenaultii* Wight, *Daphniphyllum neilgherrense* (Wight) K.Rosenthal, *Pittosporum tetraspermum* Wight & Arn., *Ilex walkeri* Wight & Gardner ex Thwaites, *Prunus ceylanica* (Wight) Miq and *Ternstroemia gymnanthera* (Wight & Arn.) Bedd. were recorded. Above 2000 m above the Anamudi base camp area, Sholas are typically found as small, fragmented patches primarily confined to gullies and depressions (Fig. 2). *Rhododendron* spp. was dominant at higher altitudes.

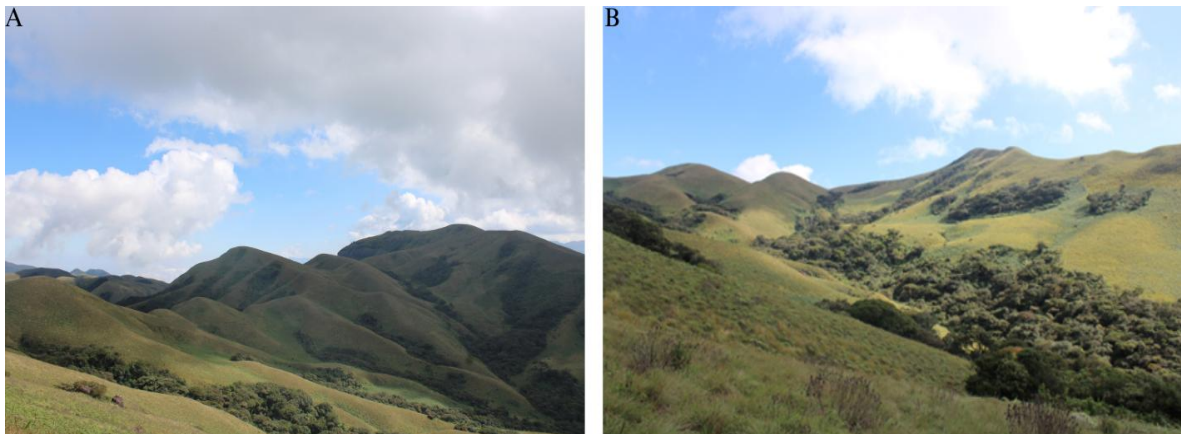


Figure 6.2 Shola patches in ENP above 2000 m asl.

Influence of altitude, patch size, species richness, and stem density on seed dispersal syndromes in Shola forests

Altitudinal effects on seed dispersal

Correlation analysis between dispersal syndromes and altitude indicated that the proportion of anemochorous species was positively correlated with altitude ($r = 0.623$, $p < 0.01$), suggesting that wind dispersal was significantly affected by increasing elevation. We observed a strong negative correlation between autochorous species and altitude ($r = -0.584$, $p < 0.01$), implying that self-dispersal mechanisms are less prevalent at higher elevations. Zoochorous species were negatively correlated with altitude ($r = -0.234$), although this relationship was weaker and lacked statistical significance. Meanwhile, ornithochorous species, characterized by bird-mediated dispersal, exhibited a significant positive correlation with altitude ($r = 0.459$, $p < 0.01$), indicating that bird-mediated seed dispersal became more prominent as elevation increased.

Influence of Shola patch size on dispersal

The studied Shola patch sizes varied from 0.05 ha to 1.26 ha. The largest patch was found in the Eighth mile (1800 m asl). A positive correlation was observed between anemochorous species and patch area ($r = 0.306$, $p < 0.05$), suggesting that wind-dispersed species were more frequently associated with larger Shola patches. A significant negative correlation ($r = -0.312$, $p < 0.05$) was found for autochorous species, indicating that self-dispersal mechanisms are more prevalent in smaller patches. Zoochorous species, which involve animal-mediated dispersal, exhibited a weak negative correlation with patch area ($r = -0.143$), although this relationship was not statistically significant. Ornithochorous species were negatively correlated with patch area ($r = -0.384$, $p < 0.05$), implying a lower frequency of bird-dispersed species in larger patches.

Species richness and stem density: implications for seed dispersal

Species numbers within each Shola patch varied from 6 to 45 species. A positive correlation between anemochorous species and species number ($r = 0.033$) was observed, whereas a slightly negative correlation with total stem density ($r = -0.030$) was noted, indicating that wind-dispersed species were not strongly associated with either fruiting species richness or

stem density (Fig.3). Autochorous species showed a weak positive correlation with species number ($r = 0.049$) and a positive correlation with stem density ($r = 0.203$), suggesting that self-dispersal mechanisms are linked to an increased number of stems. Zoochorous species showed positive correlations with both species number ($r = 0.040$) and stem density ($r = 0.108$); however, these correlations were not statistically significant. However, ornithochorous species were negatively correlated with species number ($r = -0.476$, $p < 0.01$) and stem density ($r = -0.499$, $p < 0.01$), suggesting that bird-dispersed species are less common in areas with higher species richness and stem density.

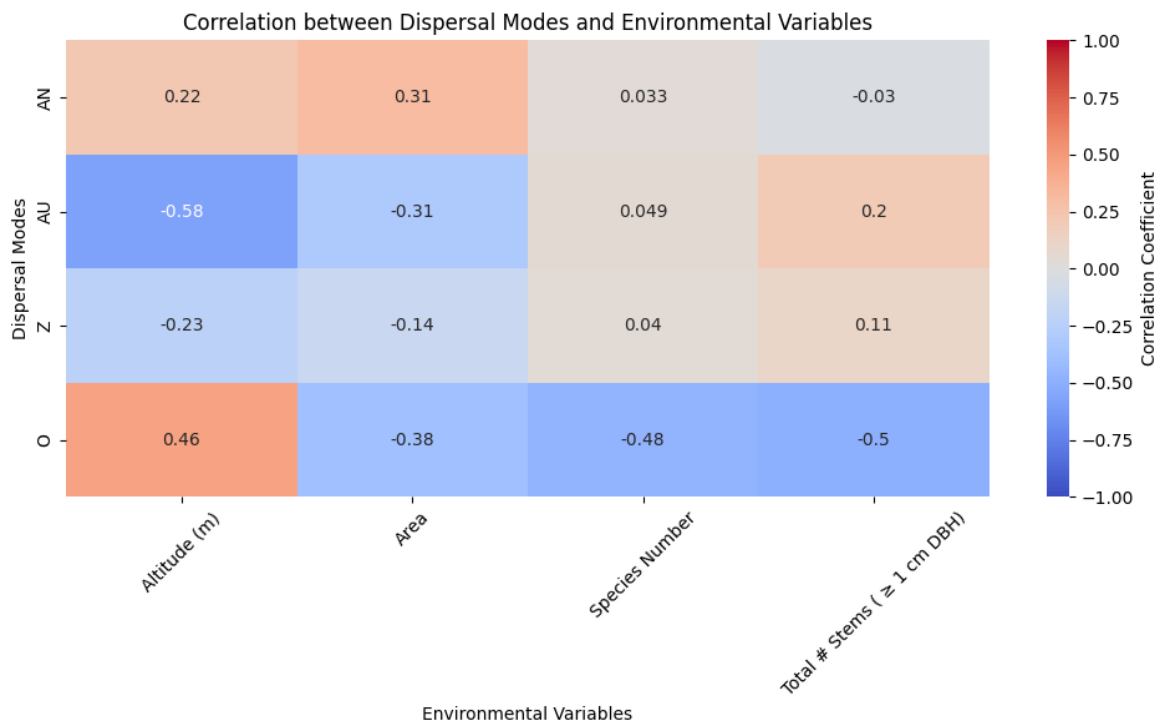


Figure 6.3 Correlation matrix of dispersal syndromes with altitude, area, species richness, and stem density

Intercorrelation analysis between dispersal modes showed a significant negative correlation between the proportion of anemochorous and autochorous species ($r = -0.409$, $p < 0.01$), indicating that as the proportion of wind-dispersed species increased, the proportion of self-dispersed species decreased, and vice versa. This suggests that these two dispersal strategies are likely functionally distinct and may occupy different ecological niches within Shola patches. No significant correlation was found between anemochory and zoochory or ornithochory, indicating that wind-dispersed species were not strongly associated with

animal- or bird-mediated dispersal. A negative correlation was observed between zoochory and ornithochory ($r = -0.420$, $p < 0.01$), suggesting that as bird-mediated dispersal increased, animal-dispersed species decreased, which could indicate competition or spatial segregation between these two animal-mediated dispersal modes within the ecosystem.

Variation in fruit and seed traits across altitudinal gradients and patch sizes in Shola

Altitude effects on fruit and seed traits

Data on fruit and seed traits across altitudinal gradients indicated a decreasing trend in both fruit and seed size with increasing altitude. Specifically, fruit length ranged from 27.4 mm at lower elevations (1704 m) to as low as 5.22 mm at higher elevations (2022 m), indicating a general decline in fruit size (Fig.4). Similarly, seed length and seed weight also exhibited a negative trend with altitude, with seed lengths ranging from 18.3 mm (1795 m) to 6.96 mm (2024 m) and seed weights varying from 2.03 g (1795 m) to 0.25 g (2024 m).

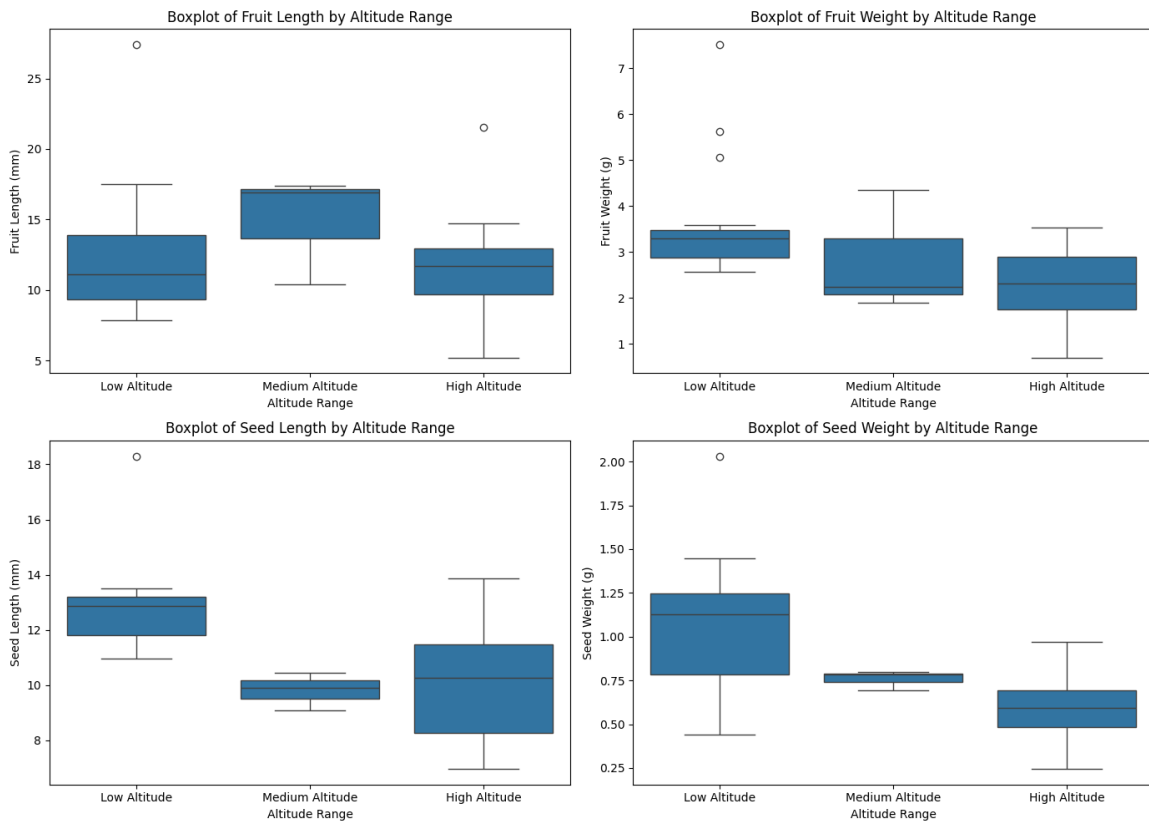


Figure 6.4 Variation in fruit and seed characteristics across altitudinal gradients in Shola patches

Influence of Shola patch size on fruit and seed characteristics

In the present study, variations in fruit length were observed across different patch sizes, with notably longer fruits (27.4 mm) being produced in smaller patches (0.1 ha). It was found that smaller patches tended to produce heavier fruits, as evidenced by a weight of 5.625 g in the 0.09 ha patch, whereas larger patches generally yielded lighter fruits (Fig.5). Seed length showed a similar trend, with larger seeds (up to 18.3 mm) being recorded in smaller patches, whereas seed lengths in larger patches ranged from 12 to 14 mm. In contrast, seed weight exhibited no clear pattern relative to patch size; lighter seeds were found in smaller patches, whereas some larger patches produced seeds weighing 0.785 g.

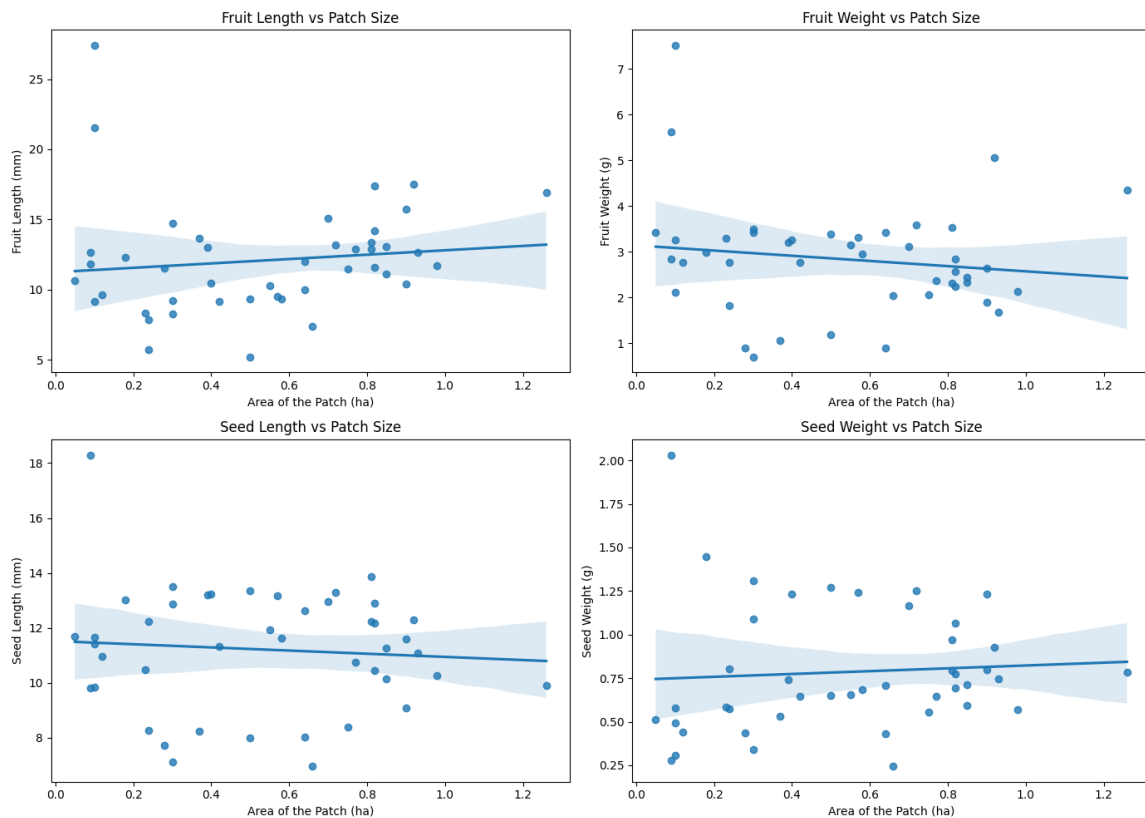


Figure 6.5 Variation in fruit and seed characteristics across different sizes of Shola patches

Correlation analysis conducted among altitude, area, and various fruit and seed characteristics in the Shola forests revealed a negative correlation between altitude and fruit length ($r = -0.227$, $p < 0.05$), indicating that altitude increases are associated with a decrease in fruit length. This trend was further explained by the negative correlations between altitude and both fruit

weight ($r = -0.548$, $p < 0.01$) and seed weight ($r = -0.596$, $p < 0.01$), suggesting that higher altitudes correspond to smaller and lighter fruits and seeds. A significant correlation was observed between fruit and seed weight ($r = 0.445$, $p < 0.01$), indicating that heavier fruits tended to produce heavier seeds. A notable relationship was observed between seed length and weight ($r = 0.805$, $p < 0.01$), suggesting that larger seeds were generally heavier. Conversely, the area of the patches demonstrated minimal influence on the studied characteristics, as indicated by the weak correlations with fruit length ($r = 0.123$), fruit weight ($r = -0.143$), and seed weight ($r = 0.070$). These low correlation values suggest that patch size does not significantly affect the morphological traits of fruits and seeds in the Shola forests.

Frugivore distribution

Frugivore density and size with altitude

Based on 195 observations, notable variability in the density of individuals per hectare was found across an altitude range of 1690 m to 2024 m. The highest recorded density of 1.11 individuals/ha was identified at 1690 m, suggesting a potential peak in frugivore activity or resource availability at this elevation. Conversely, a reduction in frugivore density was observed as the elevation increased (Fig. 6). Large-bodied fruit-eating species, such as wild boar (*Sus scrofa*), Nilgiri langur (*Semnopithecus johnii*), small Indian civet (*Viverricula indica*), and brown palm civet, were more frequently observed at lower altitudes. In contrast, smaller frugivores, including the Malabar whistling thrush (*Myophonus horsfieldii*), crimson-backed sunbird (*Leptocoma minima*), and Nilgiri flowerpecker (*Dicaeum concolor*), were observed more frequently at higher altitudes compared to larger-bodied fruit-eating species. A negative correlation between altitude and total frugivore biomass was also identified, with a coefficient of -0.034, indicating that, as altitude increased, the total frugivore biomass tended to decrease.

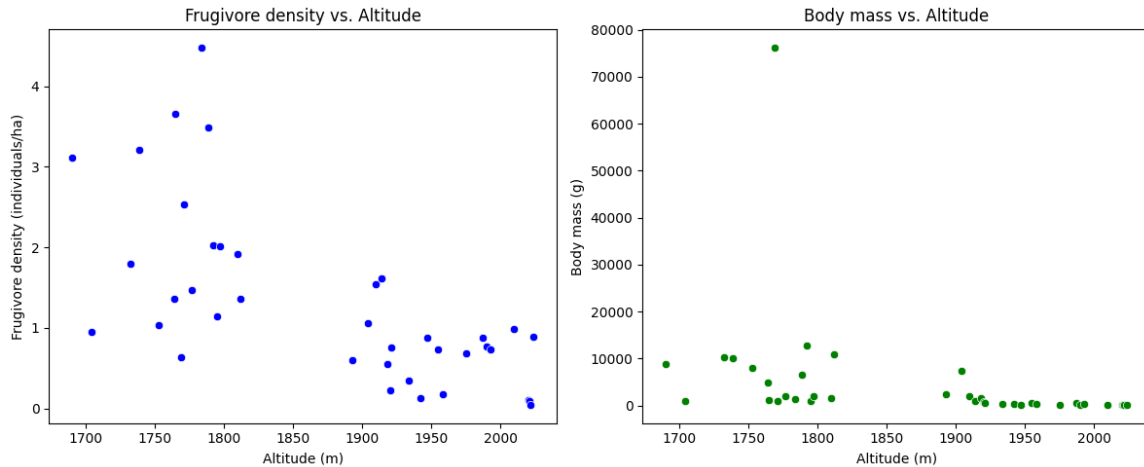


Figure 6.6 Altitude effects on frugivore density and size distribution

Rainfall and temperature effect of frugivores

Analysis of major frugivore abundance across the months (Fig. 7) showed that frugivore abundance was influenced by rainfall and the minimum and maximum temperatures. The Nilgiri wood pigeon exhibited strong positive correlations with the minimum temperature (0.895), maximum temperature (0.549), and rainfall (0.937). Similarly, the Indian cuckoo showed strong correlations with minimum temperature (0.868) and rainfall (0.953), whereas the small Indian civet showed positive correlations across all factors, particularly with minimum temperature (0.816) and rainfall (0.639). The Eurasian blackbird and Nilgiri langur showed moderate correlations with rainfall (0.744 and 0.561, respectively), indicating a preference for higher precipitation.

Red Vented Bulbul displayed negative correlations with minimum temperature (-0.525) and rainfall (-0.640). Jungle myna also showed negative correlations with maximum temperature (-0.229) and rainfall (-0.297), showing a tendency toward less warm environments. The small green barbet exhibited negative correlations with the maximum temperature (-0.596). However, the brown palm civet showed weak correlations with the environmental variables, suggesting that it was less influenced by temperature and rainfall changes.

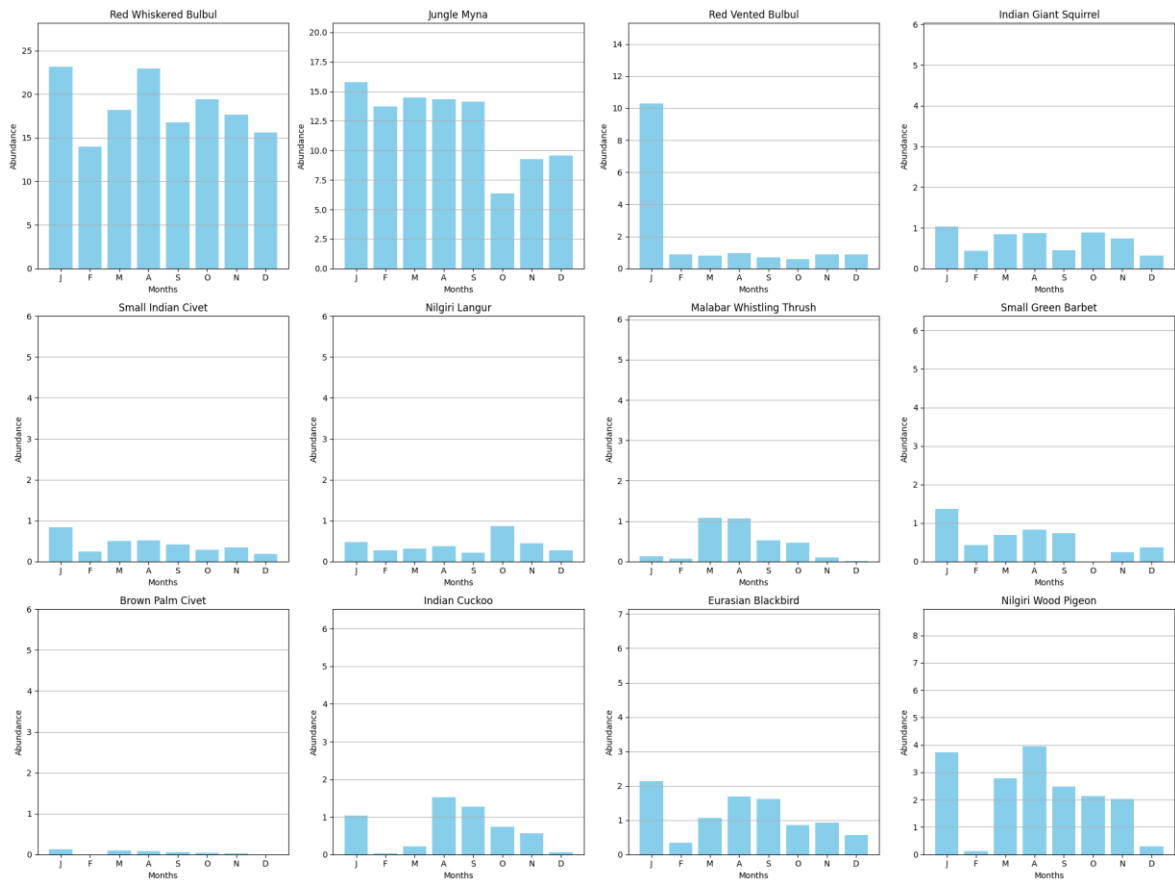


Figure 6.7 Monthly variation in frugivore abundance in ENP

Determination of plant frugivore morphological adaptations

The analysis of frugivore morphological characteristics, such as body mass and gape width, and fruit morphological characteristics, such as fruit size, fruit weight, seed size, and seed weight, indicated a significant positive correlation between frugivore body mass and gape width ($r = 0.42$, $p = 0.006$), indicating that larger-bodied frugivores tend to have wider gapes (Fig. 8).

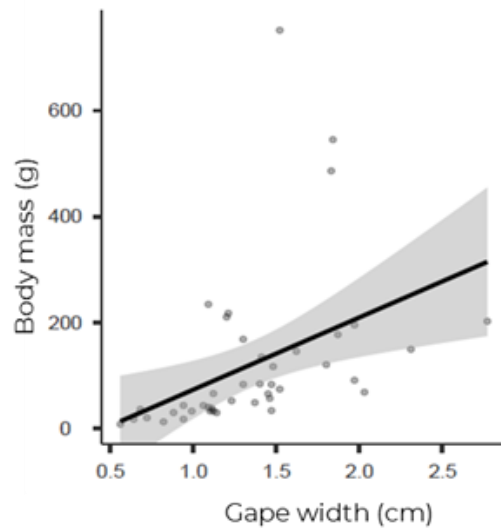


Figure 6.8 Relationship Between Frugivore Body Mass and Gape Size

Body mass was positively correlated with both length of the fruit consumed ($r = 0.3811$, $p = 0.002$) and fruit weight ($r = 0.657$, $p = 0.024$). Similarly, a strong positive relationship was identified between frugivore body mass and the length ($r = 0.716$, $p = 0.009$) and weight ($r = 0.811$, $p = 0.002$) of the seeds they consumed (Fig. 9).

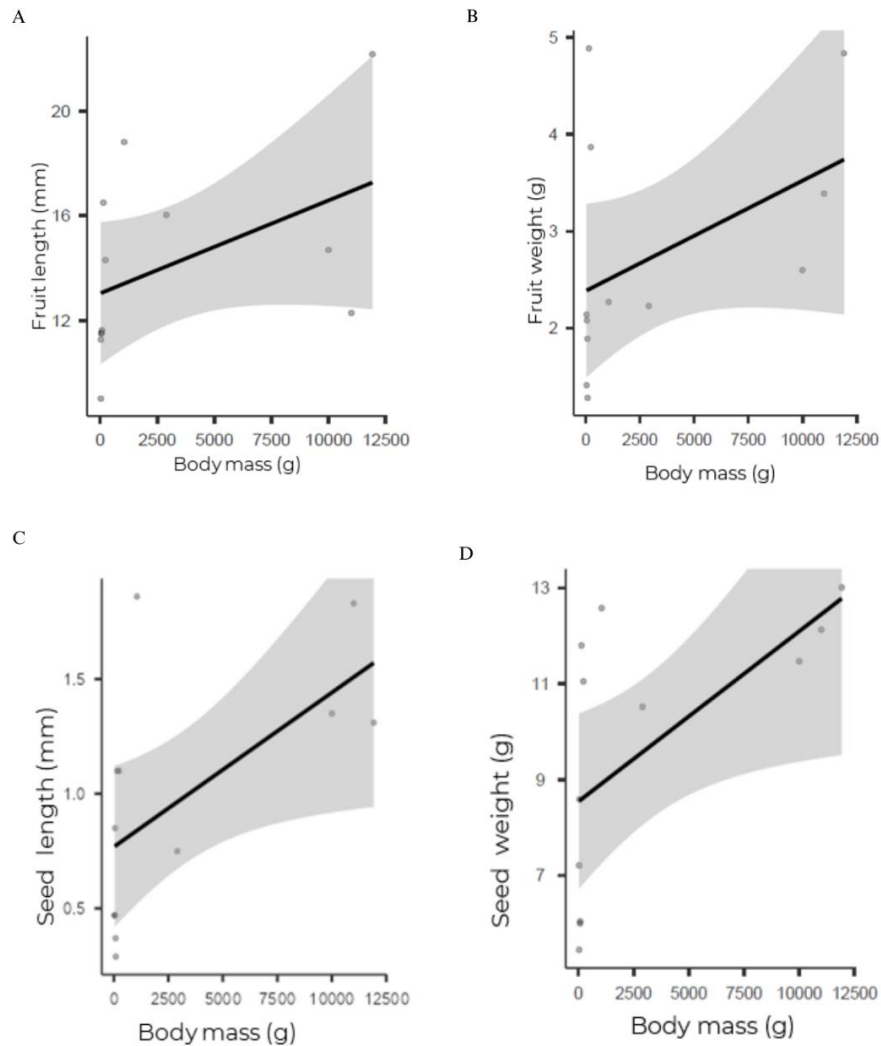


Figure 6.9 Fruit and frugivore characteristics in ENP- A) Frugivore body mass and fruit length, B) frugivore body mass and fruit weight, C) frugivore body mass and seed length, D) frugivore body mass and seed weight.

6.4 | DISCUSSION

Effect of abiotic factors on seed dispersal

Our study revealed significant patterns in the relationship between the seed-dispersal syndrome and altitude in Shola forests, suggesting that environmental gradients play a crucial role in determining dispersal strategies. The predominance of wind-dispersed species along the altitude indicates that suitable conditions for wind dispersal at higher altitudes can make this dispersal strategy more effective at higher altitudes. Our results are similar to previous studies demonstrating wind dispersal in higher altitudes. These studies show that higher

altitudes often accommodate less dense vegetation and greater wind exposure results in the predominance of wind-dispersed species (Almeida-Neto et al., 2008; Buitron-Jurado and Ramirez 2014, Duivenvoorden et al., 2012; Tackenberg, 2003). We found that self-dispersal strategies are less prevalent in higher altitudes, which is supported by the negative correlation between autochorous species and altitude. This can be due to the challenging conditions at higher altitudes including low soil nutrition, scarce resources and thus increased competition that could potentially reduce the success of autochorous species (Schupp, 1995). Our findings are supported by the idea that environments characterised by abundant resources and stability promote self-dispersal rather than varying environmental conditions that can be seen at higher altitudes (Jurado and Westboy, 1992).

The negative association observed between zoochorous species and altitude may be an indication of frugivore assemblages that vary with altitude, such as larger frugivores often found at lower elevations, where fruit availability is high (Hamann et al., 1999). We hypothesized that the distribution of zoochorous species can be affected by frugivore assemblages and availability, which might potentially complicate the interaction between altitude and seed dispersal patterns. On the other hand, the positive association between altitude and ornithochorous species highlights the importance of birds as seed dispersers at high altitudes. One possible explanation for this trend is that many birds have evolved to forage at higher altitudes, which increases their dependency on fruits as an energy resource.

The positive association between anemochorous species and patch area indicates that larger Shola patches offer favorable conditions for species dispersed by the wind. Our finding is consistent with previous studies showing that dispersal strategies might be influenced by the size of the habitat since larger areas support more plant diversity and in turn more opportunities for dispersal by wind (Nathan and Muller-Landau, 2000). The negative association between patch size and autochorous species indicated that self-dispersal is more common in smaller patches. This could be due to plant adaptations to constrained environments to ensure dispersal effectiveness and reproductive success.

There might be a competition between wind-dispersed species and species dispersed by the self-dispersal, as indicated by their negative correlation. The increase in the proportion of self-dispersed species with wind dispersal suggests that these two strategies operate in distinct

ecological niches. Our results are supported by the theory that plants can maximize their dispersal success by using different dispersal strategies under a range of environmental conditions (Schupp, 1993). The lack of any correlation between wind-dispersed species and either zoochory or ornithochory shows that species dispersed by wings are not associated with dispersal mediated by birds and animals. As per earlier studies conducted with a similar focus, different seed dispersal strategies often function independently in forest ecosystems, which is in line with our findings (Howe and Smallwood, 1982; Nathan and Muller-Landau, 2000).

Declining animal-dispersed species with increased bird-mediated dispersal can be a sign of competitive exclusion, where the presence of one dispersal mechanism adversely impacts the other. Another possibility is the spatial aggregation of species, which could result in differential habitat use by species, depending on specific dispersal mechanisms. The resilience of the plant community to environmental changes and the overall community composition can be impacted by such processes.

While Shola patch size seemed to have little impact on diaspore traits, our study found significant patterns in the relationship between altitude and fruit traits. The observed negative correlation between altitude and diaspore traits indicates that as elevation increases, plants tend to produce smaller and lighter fruits. The same pattern was observed in earlier research in TMF, where harsh environmental conditions at higher altitudes, such as lower temperature and reduced soil nutrients, limited plant growth and reproductive output (Givnish, 1999). The production of smaller fruits and seeds may be an adaptive strategy by plants in these environments to lower the energy expenditure on reproduction, which enables plants to efficiently allocate survival in challenging habitats (Körner, 2007). According to DiManno and Ostertag (2016), the availability of soil nutrients, particularly nitrogen, can be related to smaller fruit and seed size, as nitrogen is essential for fruit production. As elevation increases, the soil Nitrogen availability decreases (Carbutt et al., 2013). This decrease, combined with a general decline in the soil microbes in the TMF (Dalling et al., 2016), can lead to trade in the functional traits of the plants.

It is also possible that the changes in frugivore assemblages with elevation are connected to the decline in the fruit and seed size. Smaller frugivores such as birds are adapted to lower temperatures and lower oxygen levels and are more likely to be found at higher elevations

(McCain, 2009). This suggests that plant reproductive traits are driven by interactions between plants and the frugivores, as frugivores that are small-bodied tend to disperse smaller seeds. The positive association between seed length and weight and fruit weights and seed weight imply that larger fruits produce larger and heavier seeds. Since larger fruits are generally better at nourishing and guarding larger seeds, the findings from our study are in line with earlier studies that have found an association between fruit and seed characteristics (Leishman et al., 2000).

According to Westoby et al. (1996), larger seeds contain greater energy reserves, which supports seedling survival in challenging environments, such as those found in high altitudinal forests (Westoby et al., 1996). Patch size showed a weak association with fruit and seed traits, indicating little or no effect on the morphological characteristics of seeds and fruits in Shola forests. This finding is in contrast to some studies on fragmented landscapes, which found that small fragments are often associated with limited genetic diversity and altered reproductive qualities (Lehouck et al., 2009). The relatively small range of patch sizes considered in this study may contribute to the lack of significant differences in dispersal mechanisms with varying patch sizes, as even the largest patches examined may have been too small (Bowers and Dooley, 1991).

The variation we observed in frugivore density along the elevation was similar to previous studies showing changing species richness and abundance along with the elevation. The frugivore density peak at 1690 m indicates an ideal zone with high resources available such as the presence of fruiting species. As per the earlier studies, these mid-elevational peaks can be due to the overlap of low-elevational species and montane flora, which can lead to high resource availability and heterogeneity of the habitat capable of attracting a wide range of frugivores. (McCain, 2009). Due to the presence of lower temperatures and less primary productivity at higher elevations, species richness tends to fall, which is consistent with our observation such as the decline in frugivore density at higher elevations (Körner, 2007). Because of the availability of larger fruiting species such as *Daphniphyllum neilgherrense* (Wight) K. Rosenthal at lower elevations, large-bodied frugivores, such as civets and primates, are frequently found there. Generally, large-bodied frugivores are widely observed in areas with scarce fruit resources. Given the decline in biomass at higher elevations, smaller

frugivores such as white eyes and Nilgiri flowerpeckers require fewer resources, and they can disperse seeds at these higher elevations.

Frugivore activity and distribution in tropical habitats are greatly influenced by abiotic factors, such as elevation, temperature, and rainfall, as demonstrated in our results. For species such as Nilgiri wood pigeon and Indian cuckoo, the association between rainfall and the abundance of frugivore indicates the dependency of these species on moist environments for food availability, particularly during fruiting events triggered by rainfall availability. Rainfall improves fruit production in tropical forests (van Schaik et al., 1993; Wright and van Schaik, 1994), making it a more plentiful and reliable food source for frugivores. Our assumption that the role of temperature as the key factor in determining frugivore activity is supported by the positive association we found between minimum temperature and abundance of frugivores such as the Indian cuckoo and Nilgiri wood pigeon. These species prefer cooler microclimates, which are often linked to lower evaporation and cloud cover, thus preserving the moisture content of fruiting plants. Comparable results were observed in montane frugivores, which favor moist conditions for foraging (Blake and Loiselle, 2000).

In contrast, the negative correlations observed for species such as red-vented bulbul and jungle myna with rainfall and temperature indicated a preference for drier and warmer habitat conditions. These species may be better suited to environments with less rainfall and wider temperature changes, such as savanna or open forest settings (Shanahan et al., 2001). Their preference for certain habitats prevents them from being seen in cooler and wetter areas where frugivores such as Nilgiri wood pigeons dominate. This indicates how crucial microclimatic diversity is in forest ecosystems. Species that favor colder temperatures and rainfall can be more susceptible to climate change, especially when the temperature rises drastically and rainfall patterns change unpredictably (Colwell et al. 2008).

Determination of plant frugivore morphological adaptations

The functional linkages between frugivores and the plants they disperse are indicated by the positive correlations observed between frugivore body mass, gape width, and diaspore traits. The dispersal of larger seeds is aided by larger frugivores, which are capable of consuming larger seeds due to their broader gape width. A well-established link exists between fruit traits and frugivore morphology in tropical ecosystems. Fruit size frequently determines which

frugivores can effectively disperse seeds from the mother plant (Wheelwright, 1985; Jordano, 1995). Larger frugivores are necessary for the dispersal of larger seeds whereas smaller frugivores are incapable of dispersing them (Bollen et al., 2004; Howe and Smallwood, 1982). Ecosystem services such as seed dispersal facilitated by large frugivores are vital for the regeneration of large-seeded species (Westcott et al., 2005). Smaller frugivores such as white eyes, mynas and bulbuls often target smaller fruits due to the limited gape width. These small-bodied frugivores play a significant role in maintaining ecosystem diversity by dispersing smaller seeds, even though their capacity to disperse larger seeds is limited (Jordano, 2000). The association of larger frugivores with larger seeds and fruits and smaller frugivores with smaller fruits highlights how species complement each other in preserving plant species diversity and ecological function (Lomáscolo et al., 2008). The co-evolutionary relationship between plants and their dispersers is highlighted by the positive association between frugivore body mass, gape width, fruit size, and seed size. Numerous studies on tropical forest ecosystems have recorded the evolution of plant traits, such as fruit and seed size, in response to frugivore foraging behaviors and morphological adaptations (Herrera, 2002; Schupp, 1993). The relationship between fruit characteristics and frugivore morphology emphasizes the importance of frugivore communities for plant regeneration. The loss of larger frugivores as a result of hunting and habitat fragmentation could disproportionately affect the dispersal of large-seeded species, which has the potential to alter plant species composition over time (Peres and Palacios, 2007). The protection of large-bodied frugivores should be given high priority in conservation initiatives since their loss could disrupt the seed dispersal network and cause a decline in large-seeded plants.

6.5 | IMPLICATIONS FOR CONSERVATION

The results of this study highlight the importance of understanding how the interactions between abiotic variables, frugivore assemblages, and plant traits are significant in Shola forest conservation. Since these abiotic and biotic factors are interconnected with each other, conservation efforts should focus on protecting large and small frugivores and habitat heterogeneity across different elevations. Because there are significant differences in fruit and seed characteristics across altitudinal gradients, diverse habitats must be preserved within the Shola ecosystem. As we observed in this study higher altitudes were associated with smaller

and lighter seeds, restoration efforts should focus on sourcing suitable plant species that suit the existing frugivore community to promote successful seed dispersal and seedling establishment (Meyer et al., 2018). The frugivore population is sensitive to habitat alterations and climate change because frugivores are associated with habitat conditions. Therefore, conservation measures are needed to safeguard the habitat for both large- and smaller-bodied frugivores to preserve their ecological role in seed dispersal and forest regeneration (Bennett et al., 2015). To protect these frugivore populations and preserve the dynamics of the Shola forest ecosystem hunting and land use practices must be managed effectively. The strong relationships identified between frugivore abundance and climatic factors demand the need to monitor the impact of climate change. This will enable the development of adaptive management strategies that respond to the shifting ecological dynamics (Dalling et al., 2016). A sense of stewardship among local communities can be achieved by educating them about the significance of frugivores in maintaining the ecosystem balance. The involvement of local communities in conservation initiatives enhances the effectiveness of management strategies and encourages sustainable practices that benefit both humans and wildlife (Bennett et al., 2015). Incorporating these conservation strategies into Shola forest management will enhance the resilience of the ecosystem to changing environments.

6.6 | CONCLUSION

The complex interactions between altitude, patch size, frugivore assemblages, and plant morphological adaptations in the Shola forest ecosystem are addressed in this chapter. Significant variations in fruit and seed traits across altitudinal gradients have revealed how environmental conditions impact plant reproduction and dispersal mechanisms, which in turn affects the abundance of frugivore communities. The peak in frugivore density observed at mid-elevations highlights the importance of preserving habitat heterogeneity, which supports a variety of frugivore species and improves their seed dispersal. Given the unique ecological characteristics of these habitats and the critical roles of frugivores, such as bulbuls, mynas, and civets, our findings highlight the need to preserve this ecosystem. Continued study and adaptive management are crucial to ensure the survival of this ecosystem, as they are still under the threat of continuing anthropogenic pressure and changing climate cycles.

6.7 | RECOMMENDATIONS

1. Improving habitat connection between isolated patches is essential for maintaining frugivore populations and enhancing seed dispersal. Establishing wildlife corridors and reducing barriers to movement promote the gene flow and provide frugivores with plenty of resources.
2. Regular monitoring of frugivore populations, as well as fruit and seed availability across altitudinal gradients and different patch sizes, will assist in determining the shifts in frugivore density, species composition, and their impact on plant regeneration.
3. Promoting sustainable land use practices can reduce habitat fragmentation. Incorporating fruit-availing species in restoration activities can provide additional resources for frugivores and improve seed dispersal.

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Conclusion

This thesis synthesizes findings from four major research areas, offering a detailed understanding of the interaction between plants and frugivores, how seeds are dispersed from the parent tree, and how environmental factors affect the process of plant-frugivore interaction and seed dispersal in unique ecosystems such as Shola. Our findings highlight how different diaspore characteristics, such as fruit type, pulp type, fruit color, fruit size, seed size, fruit weight, seed weight, and nutritional characteristics, affect the interaction of frugivores with fruits, which in turn results in seed dispersal. We categorized the fruits based on dispersal mechanisms and identified the species composition in each dispersal syndrome. From the analysis of fruit morphological traits, fleshy, small, blue/black/purple fruits were predominantly dispersed in avian frugivores. Fruits that are larger and brown/grey/green in colors tend to be consumed by mammals. Species that are dispersed by wind are lighter in size and either grey or brown in color, resulting in differential seed dispersal pathways across Shola species. Large-bodied mammals show high species strength and have been found to play a crucial role in spreading larger fruits. Large frugivores, such as primates, promote seedling establishment and improve the structure and regeneration of forests. Fruit biomass production varies seasonally with respect to rainfall availability, minimum temperature, seed disperser availability, and germination conditions. The coordination of these factors emphasizes the significance of seasonal synchrony, which can foster frugivore assemblages and seed dispersal. Frugivore diet preferences and seasonality of fruiting patterns aid in forest regeneration. This shows how frugivore dependency on certain plant species is influenced by fruiting seasonality. Our investigations on the role of abiotic factors such as temperature, rainfall, elevation, and Shola patch size on seed dispersal showed that at higher elevations, frugivore abundance and diversity were limited by harsh conditions, such as low temperatures and poor soil conditions. Therefore smaller-bodied frugivores such as Nilgiri flowerpeckers, small fruits and wind-dispersed fruits were more dominant in high elevations. Lower elevations support the abundance of larger frugivores, such as jackals, squirrels, langurs, and civets, and a higher abundance of large-fruited plants. These altitudinal changes show how

plant and animal traits co-evolve to maximize seed dispersal along elevational gradients. Our results highlight the importance of frugivore diversity in ensuring the effectiveness of seed dispersal. Conservation strategies should prioritize the protection of large frugivores, which are the main dispersers of larger seeds. Our findings can aid the creation of targeted conservation plans and restoration activities in Shola ecosystems to support ecosystem health and forest resilience.

Recommendations

A coordinated approach that addresses both ecological processes and community engagement is necessary to conserve the Shola ecosystem. Avian and mammalian seed dispersers are key to forest regeneration, as they facilitate the transport of seeds to wider areas, leading to the sustainability of diverse plant populations. Therefore, it is crucial to protect the habitats of these frugivores and seed dispersers. However, it is not just about keeping the habitat suitable for these species; restoration projects in fragmented ecosystems such as Shola should actively encourage species with specific traits suitable for attracting and dispersing by local dispersers such as diaspores with particular shapes, sizes, or colors. Incorporating information on suitable plant traits and species that interact with animals and birds into restoration projects is essential. By aligning reforestation efforts with these characteristics aiding seed dispersal, restoration can tap into the existing networks of seed dispersers, improving the success of seedling establishment and promoting forest regeneration.

Establishing long-term monitoring programs is crucial for understanding the health of frugivore populations and for tracking seasonal variations in fruit production and seedling success. Such programs offer insights into the evolving relationships between frugivores, fruit availability, and seed dispersal patterns, which are especially important as ecosystems face the pressures of climate change. The observed connections between rainfall, temperature, and fruit biomass underscore the need for conservation strategies that anticipate shifts in fruiting patterns and frugivore behavior. By integrating climate projections and developing adaptive management strategies, we can help these ecosystems become more resilient and better equipped to endure climate-related challenges.

Enhancing habitat connectivity through wildlife corridors is vital for supporting gene flow and enabling frugivores to move freely across fragmented landscapes. These corridors allow frugivores to reach resources across broader areas, reduce population isolation, and strengthen genetic diversity. Restoration efforts should focus not only on reconnecting isolated forest

patches but also on restoring degraded areas, especially along altitudinal gradients where environmental conditions and available resources vary significantly.

Involving local communities is crucial for ensuring the long-term success of conservation efforts in the Shola forests. Educating residents about the vital roles that frugivores play in maintaining forest ecosystems, especially through seed dispersal, can help build local support for conservation initiatives. By highlighting the interconnectedness of wildlife and their habitats, outreach programs can raise awareness and foster a sense of responsibility for preserving the forest. Promoting sustainable land-use practices that balance farming with forest conservation is key to preventing the further fragmentation of critical habitats. Collaboration with local stakeholders, especially in managing wildlife corridors and reforestation efforts, can create a more inclusive conservation approach. When local communities actively participate in and benefit from conservation efforts, it helps to ensure the resilience of Shola forests and the biodiversity they support.

Broadening research on other tropical montane ecosystems would deepen our understanding of the complex relationships between diaspore morphology and dispersal mechanisms and highlight the diversity of adaptations found across various landscapes. Comparative studies in similar montane forests could reveal both common patterns and unique adaptations that would inform conservation efforts not only locally, but also in montane environments worldwide. Such research, paired with adaptive management practices, will be crucial in fine-tuning conservation strategies, as new challenges, particularly those driven by climate change, continue to emerge.

Effective forest management in Shola forests should also balance the need for biodiversity with the socioeconomic priorities of local communities. Sustainable forest management plans could incorporate practices, such as controlled harvesting, ecotourism, and resource-sharing initiatives, which can contribute to forest conservation while supporting the local economy. These efforts, when integrated with supportive policies at the regional and national levels, can strengthen protection measures for Shola forests, helping maintain their ecological health and resilience. Altogether, these recommendations emphasize a collaborative, informed, and adaptive approach to conserving the Shola forests' rich biodiversity and unique ecological roles in the Western Ghats.