1. Pollen and vegetation

Biodiversity is considered to be the backbone of any ecosystem to function smoothly and seamlessly (Cardinale et al. 2012). The field of biodiversity is particularly attractive for conservation biologists and ecologists because of its significant role in maintaining the stability, productivity, and functioning of an ecosystem. The factors that influence biodiversity include climate, heterogeneity of habitats, predation and competition, and availability of energy sources (Currie et al. 2004). However, the exact mechanisms by which these factors influence biodiversity in a region are unclear and the underlying causes for the ever-changing biodiversity are unknown. Efforts have been made to obtain information from plant and animal fossils regarding biodiversity in the past; however, these have failed to provide contiguous, clear, and precise information (Benton 2000).

An ecosystem is largely influenced by the diversity of species pertaining to that ecosystem especially for shorter timescales and dynamic ecosystems. In case of larger timescales and ecosystems that do not change over time, it is difficult to assess the impact of biodiversity on the characteristic features of the ecosystem. In such scenarios, analysis of pollen provides a comprehensive investigation tool to study the different types of vegetation in a region and relate that to the surrounding ecosystem (Matthias et al. 2015). Fossil pollen obtained from sediment samples can provide valuable insights regarding plant species diversity, and studies have analyzed both pollen number as well as species in available samples (Bush and Colinvaux 1990).

1.1 Use of pollen to study biodiversity

For each sample of pollen obtained, the number of different types of pollen varies with time and statistical analysis of these variations indicates changes in the surrounding landscape (Birks and Line 1992). For instance, a higher number of pollen types in the sample indicate that the land has been used by humans since centuries for cultivating different types of plants and crops. It could also indicate recent changes in the landscape, high floristic richness especially where flowering plants lack species diversity, and presence of higher taxa of plant types in the region (Mazaris et al. 2010). Diversity indices have also been formulated based on two important characteristic features of pollen – richness and abundance. Different indices have assigned different degrees of significance to these two features on the basis of the region being investigated and the species diversity of the vegetation being studied. Other factors that might influence the formulation of these diversity indices include productivity of pollen, ability of pollen to get dispersed easily, and sediment accumulation rate of pollen. Despite these challenges, a combination of the number and species diversity of pollen can provide valuable insights into the past vegetation of the region (Purvis and Hector 2000).

1.2 Use of pollen to study climate

One of the biggest indicators of the geographical distribution of different vegetation types is climate as every plant has different requirements and tolerance levels for extreme temperatures. Therefore, it can be assumed that climatic changes in the past had a major influence on the growth and distribution of terrestrial plants. These alterations in plant distribution can be analyzed in-depth by studying the fossil pollen records reconstructed with inputs from peat bogs and lake sediments

(Woodward 1987). Despite the fact that fossil pollen records give several insights regarding the local vegetation, this is not always a fool-proof method for relating climatic variations with surrounding plants. This is because pollen profiles obtained from lake sediments are not always reliable as the formation, dispersion, and preservation of pollen can vary immensely between different species of plants. One way in which this relationship can be made clearer is by reconstructing information obtained from modern pollen and relating it to modern climatic variations, and then extrapolating the results to information obtained from fossil pollen (Brewer et al. 2007).

Analogues of modern pollen have been extensively used for paleoecological reconstructions and paleo-records have been calibrated using the relationship between pollen trap data and vegetation (Huntley et al. 2011). These types of studies are quantitative and can be used to accurately draw relationships between pollen, altitudes, and climatic conditions for studying the vegetation of a region. For example, extensive pollen-rain studies have been conducted in tropical regions such as Africa in order to study and differentiate types of vegetation along gradients of latitudes and altitudes (Watrin et al. 2007). Results of these studies have demonstrated that pollen spectra tend to be similar to other spectra obtained from the same vegetation zones and differ from spectra obtained from other vegetation zones. This implies that pollen spectra are unique to vegetation zones and reconstructing vegetation profiles in one region cannot give useful insights about vegetation profiles in other regions around the world (Gajewski et al. 2002). This conclusion has been reinstated by another study conducted by Urrego et al. (2011) who studied the relationship between pollen-rain and vegetation in the Neotropical region and found that pollen spectra from this region threw light on the past vegetation profiles of Amazonian montane forests. However, insights obtained about vegetation types from pollen spectra are extensive for the specific region and provide in-depth information about the altitudinal distribution of vegetation in the modern age (Niemann et al. 2010).

1.3 Challenges in using pollen to understand biodiversity

In an ideal scenario, all the different varieties of pollen are detected and correctly identified, and information obtained regarding pollen diversity is directly indicative of plant diversity in the region (Weng et al. 2006). However, the use of pollen to understand and analyze the types of vegetation in a region is not straightforward and is filled with several challenges. Taxonomically, plant types have not been accurately classified and this poses a challenge to understanding the diversity in species of plants in a specific region. Additionally, pollen of different species of plants show variations in formation and dispersal, and so results obtained from one plant species cannot be extrapolated to other plant species (Giesecke et al. 2014). The diversity of pollen cannot always be correlated with the diversity of plants because all species of pollen have not been documented clearly. Also, many plants belonging to the entomophilous taxa are 'silent', meaning that they are not well-represented on pollen spectra. As a result, pollen diversity may either over-represent or under-represent plant diversity and an understanding of this issue is necessary to correctly interpret pollen spectra (Faegri and Iversen 1989).

2. Modern pollen analysis

In paleoecology, fossil pollen and their spores are collected and analyzed to understand biodiversity in plants and variations in vegetation based on climatic variations in the region. In order to use fossil pollen accurately, it is essential to have an in-depth understanding of the representation of plant diversity in pollen samples. Modern pollen analysis uses modern analogue techniques wherein a comparative analysis is conducted between fossil pollen samples and modern pollen samples in order to understand changes in landscape, climate, and vegetation (Barboni et al. 2004). Another advantage of modern pollen analysis is to understand the productivity of pollen of different plant species which can enhance our interpretation of fossil pollen spectra (Soepboer et al. 2007).

2.1 Brief history of modern pollen analysis

The practice of analyzing modern pollen samples began in Europe in the 19th century with the establishment of the European pollen monitoring programme. Eventually, ecologists started conducting extensive studies using modern pollen rain which was collected by means of Tauber traps (Hicks et al. 1996). The early 1970s saw the use of modern pollen analysis in the Neotropics and the sophistication of collection and analysis methods of modern pollen. The source of pollen samples shifted from peat deposits to lake sediments and laboratory techniques evolved with the development of modern technologies. Despite the rising interest in modern pollen analysis by ecologists around the world, fossil pollen analysis was still the preferred choice for archeobotanical studies, studies of past vegetation in central Europe, and interglacial studies. This changed with the formulation of concepts such as glacial-interglacial cycle, use of intrinsic ecological processes for studying forest development in the early Holocene period, and spatial scale and resolution. Today, several important and unrelated developments have helped enhance the value of modern pollen analysis. These include sophistications in electron microscopy, preparation of large-scale reference pollen collections, and use of fast and accurate computing techniques to interpret data and perform complex statistical analyses (Birks and Berglund 2016).

2.2 Importance of modern pollen analysis for understanding pollen-vegetation relationship

Until recently, fossil pollen samples were used to reconstruct Quarternary environments, understand the distribution patterns of past vegetation, and consequentially gain insights into past climatic variations. However, it has become increasingly apparent that modern pollen analysis is essential to interpret the results of fossil pollen analysis by analyzing the composition of modern pollen-rain samples. Today, ecologists compare fossil pollen data with pollen data acquired from local vegetation in order to understand the growth patterns of vegetation in the past. The investigations may be either qualitative or quantitative or both, and variations in pollen spectra are used to draw conclusions regarding variations of vegetation diversity in the past (Jackson et al. 1995).

Earlier, fossil pollen analysis was never conducted in tropical regions due to the immense diversity of vegetation in these regions. With the increasing use of modern pollen analysis, this became possible and was first undertaken by Flenley (1973) who analyzed modern pollen rain samples in the tropical regions. It is often seen that several species of tropical plants are not represented in fossil pollen spectra; however, use of modern pollen analysis could identify several such pollen species and relate them to vegetation found in these regions. Therefore, it has been concluded that using modern pollen spectra from samples obtained from various regions that are diverse in their climatic conditions and altitudes can remove some of the uncertainty that arises from studying fossil pollen spectra (Quamar and Kar 2019).

An important reason for studying pollen-vegetation relationships is to predict future changes in vegetation in response to climatic variations. Modern pollen analysis helps ecologists develop vegetation-climate models that can be compared with known data and used for predictions of future vegetation distribution (Ni et al. 2000). Despite the fact that fossil pollen records provide direct correlation with past vegetation distribution patterns, modern pollen analysis helps in accurate interpretation of fossil pollen data. Not only this, but analysis of modern pollen samples helps extrapolate data to a continental level and shorter or longer time ranges. Several studies have reported the use of modern pollen analysis for large-scale reconstructions of past vegetation (Marchant et al. 2001; Paez et al. 2001).

2.3 Effects of climatic changes on vegetation diversity

In the last 50 years, climate on Earth has seen humongous changes that have resulted in extreme variations in the distribution and physiology of vegetation (Thuiller et al. 2005). These variations are consistent with theoretical models of change and point towards significant harm caused to the environment due to climatic anomalies. Climatic changes have been predicted to have a major impact on the distribution and diversity of plants at a global level, and thereby bring about changes in ecosystem biodiversity (Bakkenes et al. 2002). As a result of changes in temperature and rainfall, many plant species are unable to survive in their natural habitats and their growth locations may get altered to regions that are more suitable for their climatic requirements. Some species may show physiological adaptations and continue to survive in their original growth regions but in limited areas. Species of weeds generally disperse pollen more rapidly and hence, they can alter their growth locations faster bringing about major and sudden changes to local ecosystems (Araujo et al. 2011). Studying ecological responses to global climatic variations can give valuable insights into biodiversity, help identify negative impacts, and predict future vegetation distribution patterns. These types of studies are possible by pollen analysis as dispersal patterns of pollen are directly correlational to distribution patterns of plants (Hassen and Dale 2001).

The last few years have seen a sudden increase in carbon dioxide levels of the atmosphere and this has had a huge impact on plant diversity due to their differential sensitivity to carbon dioxide levels (Grunzweig and Korner 2001). The increase in carbon dioxide and other gases in the atmosphere is related to a proportional increase in global temperature. It has been predicted that if the global temperature continues to rise, plant species located in the Northern hemisphere might have to move to regions of higher altitude and colder temperatures in order to survive and thrive (Kappelle et al. 1999).

According to the plan of nature, every plant species has a specific range of temperature, humidity, rainfall, and gas levels within which it can grow comfortably. With increase in temperatures on Earth, the natural distribution of species is affected and plant species are expected to shift their locations to regions that match their growth requirements. However, not all plant species are capable of migration and those species that are unable to migrate from their current location face the risk of extinction. Studies that can throw light on the relationships between climate change and plant diversity, and predict future changes in plant distribution can inform the development of strategies to enable plant migration so that their survival and growth rates are not affected. Again, this may not be possible for all plant species and/or regions, and considerable research is required to determine the impact of climatic changes on plant diversity in these regions (Desanker 2002).

2.4 Effects of human activities on vegetation diversity

Since the past few decades, the rapid growth in technology development and urbanization has had wide-ranging impacts on the surrounding environment and its local ecosystems. The reason for this is that humans have started using large areas of land, destroying landscape components in the process, to promote their commercial activities (Su et al. 2012). Another reason is immense population explosion especially in developing countries around the world. This has led to the use and destruction of forest land for building houses, constructing roads, establishing pipelines, and promoting intense use of transport in these areas. As a result of these activities, the natural flora of several regions has been vastly disturbed and a considerable number of species of wild plants have been uprooted from their natural habitats. Today, human impact activities are considered to be the most significant reason for ecological disturbances that have started appearing at a global scale (Alberti 2008).

Specifically, human activities have affected the concentrations of major and minor nutrients in the soil that have, in turn, impacted the diversity and productivity of local ecosystems. There has been a considerable increase in the rates at which nitrogen is added to the soil and phosphorous is released from the soil. Increased deposition of acids in the soil has led to high rates of leaching which has, in turn, led to a decline in calcium levels in the soil (Tilman and Lehman 2001). In order to maintain natural distribution patterns of vegetation, nature has created several biogeographic barriers for pollen dispersal outside their natural habitat. Human impact activities have intentionally or unintentionally removed these barriers leading to changes in pollen dispersal patterns and growth of plant species outside their natural growth environment (Lonsdale 1999).

Although commercial human activities have far-reaching impacts on the environment, climate, and biodiversity, there are limited theoretical models that can help predict the impact of human activities on biodiversity. The models that do exist only help us understand the relationship between human activities and its impact on the environment. However, the specific impact on the distribution and survival of plant species as a result of human activities is largely lacking. The loss of biodiversity is not synonymous with environmental or ecosystem variations and therefore cannot be extrapolated from these, more general, predictions. For instance, ascertaining degree of loss of biodiversity by measuring the decrease in number of local plant species cannot be predicted by generic models because this will depend upon the original number of plant species that are a part of the local ecosystem. Therefore, spatial relationships between plant species are more important in predicting changes in biodiversity as compared to generic models that predict environmental and ecological impacts (McNeely et al. 1996).

2.5 Representation of human impact activities in pollen spectra

As a result of the far-reaching impacts of destructive human activities on the local ecosystems, it has become paramount to understand the extent of impact caused by these activities at various temporal and spatial scales. These types of investigations can help us develop an in-depth understanding of the ecological hierarchy and ecosystems, and discern its evolution under the influence of human activities (Franco-Gaviria et al. 2018). One of the most important tools for achieving this is by means of pollen analysis that can help us recreate distribution patterns of past vegetation and correlate these patterns with current plant growth patterns observed both regionally and globally (Delcourt and Delcourt 1991).

Some of the important parameters that are used to assess human activities in an ecosystem are changes in types and numbers of tree pollen, pollen records of cereal crops and weeds, and increase in numbers of pollen from species growing in pastures and meadows. Pollen spectra of regions where increased infiltration of nitrogen in soil occurs may show the appearance of ruderal plants such as *Artemisia* and *Rumex*, as these plants are sensitive to changes in the nitrogen content of the soil. Appearance of species from the goosefoot family in the pollen spectra may indicate human activities at the sea level. On the other hand, pollen spectra from regions with low levels of destructive human activities may show the presence of plantains and *Cerealia*-type plants as they are related to the practice of animal husbandry. If the pollen spectra show the presence of species of deciduous trees belonging to the genera *Tilia* and *Ulmus*, it is indicative of the occurrence of human activities since the late Atlantic period (Miotk-Szpiganowicz et al. 2010).

If the pollen spectra show increase in representation of cereal crops such as wheat and decrease in representation of deciduous species, it is indicative of deforestation of large areas and a simultaneous increase in practices of agriculture. Pollen spectra from regions which have undergone intense human activities demonstrate the presence of plant species that are connected to agriculture and animal husbandry. The specific plant species that are observed in pollen samples may vary from region to region; however, the genera of plants found in different regions can be correlated in relation to the degree of human activities that have taken place. For instance, pollen spectra from areas of northern Poland show the presence of rye as rye farming has been a historical practice in this region (Miotk-Szpiganowicz et al. 2010).

The regions that are most commonly affected by human activities include uncultivated lands and farmlands, and pollen spectra of these regions are representative of plant species affected by urbanization practices. The pollen species that are found to be dominant in these regions include crop species belonging to the families Brassicaceae and Poaceae (Yang et al. 2012). Uncultivated lands specifically show an increase in prevalence of pollen species that are considered to belong to human-companion plants such as Chenopodiaceae and *Artemisia*. Pollen spectra from large areas of uncultivated land often represent diversity of pollen species at the boundaries where these lands transition into areas of natural vegetation (Shu et al. 2010). In general, human impact is directly measured by variations in pollen of trees, cereals, and human-companion plants in pollen spectra. However, the representation of various pollen taxa in the pollen spectra can vary based on the region from which the samples are collected and the extent of impact that human activities have had in the region (Li et al. 2015).

Forests and grasslands are areas that have not borne the brunt of commercial human activities, and pollen spectra from these regions show characteristic patterns of plant distribution. Pollen spectra from forest areas show a high prevalence of pollen from *Larix*, *Betula*, and *Quercus*. On the other hand, *Pinus*, *Carpinus*, and Elaeagnaceae show low indicator values in pollen spectra of forests which may be attributed to high rates of dispersal and over-representation in the pollen samples (Xu et al. 2007). The pollen spectra of grasslands may represent up to 12 different pollen taxa belonging to the families Asteraceae, Polygonaceae, Convolvulaceae, Liliaceae, and *Nitraria* to name a few. Pollen from the Convolvulaceae family has the largest indicator value for grasslands and these pollen taxa are commonly found in grassland areas with minimal human activities (Li et al. 2015).

3. Comparison of vegetation diversity in the Holocene and Last Glacial periods

The period from the Last Glacial to the early Holocene marks a period of rapid and tremendous climate change and consequentially environmental change which has altered global conditions from glacial to interglacial. As this was the last climatic transition witnessed by the planet, understanding climatic changes and its effect on biodiversity is important to understand the present scenario and to predict future landscape changes (Orombelli and Ravazzi 1996). Biodiversity is always affected due to changes in the global climatic conditions and several patterns of vegetation distribution in response to climatic changes have emerged over time (Svenning et al. 2015).

3.1 The Last Glacial period

During the initial glacial periods, significant changes in climatic conditions led to complete extinction of several global and regional species of plants. Several trees in Europe and Australia, and molluscs in the Mediterranean, North Sea, and California have become extinct (Bowersox 2005). As the glacial period progressed towards its later stages, the extinction of plant species continued although at a comparatively lower rate. This can be attributed to the fact that plant taxa that were sensitive to changes in ecological systems and climate had already disappeared in the early glacial period. Examples of species that became extinct during this period include *Zelkova*, an ulmaceous tree in Europe, and *Picea critchfieldii*, a spruce tree belonging to North America (Jackson and Weng 1999).

The last glacial period has been placed at around 20,000 years ago and lasted for around 2,000 years at which time the climatic conditions of many regions around the world were similar. This was also the period when the largest amount of ice was present on the planet, the global temperatures were lowest, the carbon dioxide concentrations in the atmosphere were low, and aridity was at its highest (Ray and Adams 2001). The climate in North America was extremely cold and the plant species that grew here included alpine tundra, spruce, fir, pine, and woodlands. Comparatively, the climate of South America was warmer and drier, as a result of which the areas of the Amazonian rainforest and Brazilian Atlantic forest were quite reduced. Also, the warm and dry climate resulted in the formation of several desert and semi-desert regions which later developed into scrub zones and grasslands (Stude et al. 1995). In contrast to the current period, Africa was slightly cooler and comparatively much drier during the last glacial period. The desert covers of the Sahara and the Namibia were greatly expanded and a negligible area of the continent was covered with forests. In contrast, Europe was covered with ice to a large extent and the vegetation found here included tundra, grasslands, and trees similar to those found in semi-desert areas (Ray and Adams 2001).

Fossil pollen analysis of samples from European regions found high prevalence of steppe tundra, shrub tundra, and polar desert tundra. Pollen samples from central and southern regions of Europe showed the presence of coniferous trees and open park tundra whereas samples from the Mediterranean region showed the presence of deciduous woodlands. In general, deciduous trees were mostly confined to forest areas mostly in southern and southeastern regions of Europe (Birks and Willis 2008).

3.2 The Holocene period

The Holocene period, so far, is considered too short for large-scale speciation or extinctions to have taken place on a global scale (Lister 2004). Although no species extinctions have been reported yet for this period, ecosystem dynamics at the regional level has been observed in several cases. Several species have been reported to have migrated to the poles or regions of colder temperatures and higher altitudes in response to global warming (Sommer et al. 2014). As a result, the species diversity in the forest regions of the upper and lower peninsulas had markedly increased due to migration of plant species from warmer regions. By this time, global warming had started promoting the melting of large pieces of ice causing the ice front to move farther up towards the poles. Also, the water from melted ice had dried up due to warmer temperatures allowing the survival of plant species that had migrated from other regions (Webb et al. 2004). Initially, these forest regions were filled with spruce trees which were later replaced by conifers, pines, and deciduous trees such as birch, ironwood, and elm (Kapp 1999). The result of this species migration was the development of a mixed type of forest with conifers and northern hardwood and the predominance of deciduous trees in the Lower Peninsula regions. On the other hand, spruce was the dominant tree in the Upper Peninsula regions that later included pine trees. This led to the formation of characteristic mixed spruce-pine forests in the Upper Peninsula (Booth et al. 2002).

The vegetation types present in the early Holocene period provide valuable insights about the climate in that they reflect cool and wet climatic conditions. As the global climate was slowly experiencing an increase in temperature, many of the plant species from rainforests have migrated to regions of higher altitudes due to their inability to survive in hot temperatures. For instance, species of tree ferns such as *Cyathea* have migrated to more humid regions as evident from analysis of pollen samples acquired from these regions. Thus, the vegetation in the early Holocene period is characteristic of the beginnings of global warming and a shift of several plant species to regions of higher altitudes (Niemann and Behling 2008).

Eventually, the numbers of pine trees decreased and these were replaced with oak trees as these are more suitable for survival in a warm and dry climate. Therefore, the increase in number of oak trees points towards increase in temperatures and decrease in humidity (Wolf 2004). In certain deciduous forests, maple trees started growing too, and as maple trees require humid conditions for growth, their presence indicated an increase in humidity in regions where these trees dominated. Meanwhile, spruce trees started migrating towards cooler regions in the north in response to global increase in temperatures, and contrary to earlier time periods, spruce trees became a scarcity in forest regions of the Upper Peninsula (Liu 1990).

3.3 Transition between Last Glacial period and Holocene period

The characteristic features of climatic conditions and vegetation distribution patterns have been ascertained for different regions during the Last Glacial and the Holocene periods. However, there are several aspects that have come to light in recent investigations that help us understand the migration and speciation patterns of plants in various regions around the world. Towards the end of the last glacial period, several species of plants and trees had migrated to cooler regions northwards towards the poles. This shift in location has been observed in recent times too with the sudden and rapid increase in global temperatures. Based on this, several species distribution models (SDMs) have been generated that provide insights regarding the distribution patterns of plants during the last glacial period (Giesecke et al. 2019).

The concentration of vegetation species in regions of lower latitudes of the Earth has led to the formation of a latitudinal gradient in terms of richness and diversity of plant species. With the continuous rise in temperatures and the consequent shift of plant species towards the poles, the generated latitudinal gradients provide a strong model for studying latitudinal climatic variations and the response of plants to climatic changes (Thomas et al. 2004). In addition to migration of plant species, several changes have occurred in the composition and physiological adaptability of the plant species too. This is also directly correlated to climatic changes and other ecosystem changes and can be deduced by pollen analysis of samples from these areas (Giesecke et al. 2019).

4. Conclusions

To achieve a clear and concise idea of all concepts discussed above, a comparative analysis between modern pollen and fossil pollen can give tremendous insights into the distribution patterns of vegetation in different parts of the world. These distribution patterns vary with changes in climatic conditions of our planet which in turn is impacted by human activities that cause harmful effects to the environment. As the past few years have seen huge variations in climate, the pattern of growth and migration of plant species has also undergone major alterations, some of them even going extinct. Studying the changes in plant distribution patterns of the past is significant as it can help us understand the underlying causes for which plant species become extinct and predict future changes in vegetation distribution in response to climatic changes. There are several limitations to pollen analysis, one of them being that it can only provide information about the taxa and not about the plant species. Despite these limitations, it is the best available method currently to study patterns of vegetation distribution and activities that impact this distribution.

5. Aims and Objectives

Having discussed the changes in vegetation diversity brought about by climatic changes and human activities, and the use of modern pollen analysis to study vegetation diversity, this thesis aims to answer the following questions:

1. What is the degree to which the composition of pollen samples from moss polsters correlates with the composition of plant taxa in the surrounding vegetation?
2. Can the pollen diversity observed in the sample be correlated with the species diversity in the surrounding landscape? If yes, to what extent can the components – richness and evenness – of pollen diversity be correlated with the species diversity of the surrounding vegetation?
3. Is there any correspondence between the main gradients as revealed by analysis of pollen assemblages and surrounding vegetation?
4. Can the correspondence of this pollen-vegetation diversity be detected from pollen samples obtained from two different time periods with different climates and geographical locations, for example, Holocene sample from northern Greece (Tristinika) and Late Glacial sample from Romania (Mohos)?

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