Ecological Modelling 359 (2017) 246–257

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

A network theoretic study of ecological connectivity in Western Himalayas

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ARTICLE INFO

Article history:
Received 19 December 2016
Received in revised form 31 May 2017
Accepted 31 May 2017

Keywords:
Ecological networks
Centrality index
Scale-free network
Small-world network
Assortative mixing
GIS

ABSTRACT

Network theoretic approach has been used to model and study the flow of ecological information, growth and connectivity on landscape level of anemochory (wind dispersal) of Himalayan moist temperate forest species in the Western Himalaya region. A network is formally defined and derived for seed dispersion model of target floral species where vertices represent habitat patches which are connected by an edge if the distance between the patches is less than a threshold distance. We define centrality of a network and computationally identify the habitat patches that are central to the process of seed dispersion to occur across the network. These central patches are located on map and geographical regions critically important for the flow of ecological information across the network are identified as Gharwal region and eastern Himachal Pradesh of Indian Himalaya. We find that the network of habitat patches is a scale-free network and at the same time it also displays small-world property characterized by high clustering and low average shortest path length. As a result, ecological information propagates rapidly and evenly on a local scale. Hubs in the network are identified as important centres for dissemination of ecological information (seeds) and need to be conserved against a potential attack by malicious agents and also ecological shocks. The network showcase a well-formed community structure. As a consequence of these structural properties of the network, anemochory floral species studied in this work are likely to thrive across the ecological network of forest patches in the Western Himalaya region over time.

1. Introduction

Almost all the natural ecosystems on earth are experiencing degradation and destruction due to human activities. In many of the landscapes, large tracts of contiguous forests no longer exists and remnant natural habitats occur as a mosaic of large and small forest patches. For sustaining the ecosystem processes, a robust movement of energy, information and materials across the network is a prerequisite. In a fragmented landscape, the forest patch connectivity is important for unhindered movement of energy, information and materials. Understanding the functional connectivity of the patches, can provide invaluable information on the conservation policy to be followed as these provide the stepping stones for dispersal and movement of various species across the landscape (Bascompte et al., 2003; Olesen et al., 2011; Jordano et al., 2003; Thebault and Fontaine, 2010).

Landscape connectivity is important in promoting the survival and vitality of species through flow of ecological information in the form of organism movement, seed dispersal and other ecological processes (Taylor et al., 2006). Maintaining connectivity and mitigating the fragmentation of habitat may be critical for landscape process such as gene flow and dispersal (Crooks and Sanjayan, 2006). One of the most formal means to explore, examine and understand the essential structural and functional dynamics of ecological complexity is provided by a complex network-theoretic (and graph-theoretic) approach to ecosystem analysis (Bascompte and Jordano, 2007; Ings, 2009; Olesen et al., 2007; Bascompte, 2009; Pilosof et al., 2016).

Our effort is essentially to realize the western Himalaya forest ecosystem as a complex system. For this we identify the individual habitat patches (entities) of the focal species and try to gain an understanding of the interactions they undergo, thus giving rise to

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http://dx.doi.org/10.1016/j.ecolmodel.2017.05.027
0304-3800/

various characteristics of the forest system that they are embedded in. Use of graph-theoretic network analysis provides relevant quantitative measures to analyse the landscape and responds directly to the level of isolation of the forest fragments in a changing landscape (Cantwell and Forman, 1993; Fall et al., 2007; Gastner and Newman, 2006; Minor and Urban, 2007; Minor and Urban, 2008; Urban and Keitt, 2001; Chetkiewicz et al., 2006). Advancements in ecological network flow modelling has led to the foundation of Ecological/Ecosystem Network Analysis (ENA), a method to holistically analyse environmental interactions (Patten, 1978; Patten, 1981; Patten, 1982; Patten, 1985; Fath and Patten, 1999; Roy et al., 2016; Ulanowicz, 1983; Ulanowicz, 1986; Ulanowicz, 1997; Fath et al., 2013). Network analysis methods to evaluate consumer – response relations have been developed and studied to find direct and indirect ecological relations between ecological compartments (Ulanowicz, 2004; Scharler and Fath, 2009).

We apply concepts from the theory of complex networks to study the level of connectivity of the major wind pollinated Himalayan moist deciduous forests that prominently include species such as *Abies pindrow (Himalayan Fir), Betula utilis (Bhoj patra/Himalayan birch)* and *Taxus wallichiana (Himalayan yew).* These floral species are wide spread in the Western Himalaya, occupying an elevation range from 1800 to 4500 m and prefer an average temperature variation range of $4^{\circ} - 24^{\circ}$ Celsius.

Since these are endemic species and are also sensitive to climate change, a break in the connectivity of these anemochory species can result in a local extinction in climate change scenario (Stocker et al., 2013). Thus one of our main objective in this work is to identify habitat patches which are critically important in conservation of the ecological network that is responsible for creating connectivity among the populations of these anemochory floral species over the last three decades (1985–2014) in Western Himalayas. One of the ways to identify potential areas of spread of anemochory plant species is through modelling their distribution. Spatial modelling for species distribution is frequently being used for management of natural resources by environmentalists (Stohlgren et al., 2010). The importance of dispersal and movement of species through the landscape have been emphasized in the developments in metapopulation biology and landscape ecology, with species populations interacting dynamically through landscape-scale movements (Taylor et al., 1993; Hanski and Gilpin, 1997; Vos et al., 2002; Vos et al., 2001). The restriction of gene flow and dispersal results in isolated populations, which is expected to result in the loss of genetic diversity (Keyghobadi, 2007). The efficacy and advantages of network theoretic approach to landscape analysis to assess the importance of individual landscape elements and to guide conservation and restoration efforts have been discussed in the scholarship (Bodin and Norberg, 2007; Estrada and Bodin, 2008; Bascompte et al., 2006).

Networks are generic representations of complex systems in which the underlying topology is a graph. Networks are generally used to model empirical data from real world problems where the relationship between given components is of importance and may evolve with time. Formally a network N is a four tuple (V_λ, E_λ, ψ_λ, Λ) along with an algorithm A such that for $\Lambda \neq \phi$, $i \in \Lambda$, V_λ is a set of vertices V_i, E_λ is a set of edges E_i, ψ_λ is incidence function $\psi_i : E \rightarrow [V]^2$ where $[V]^2$ is the set of not necessarily distinct unordered pairs of vertices such that $\left(V_i, E_i, \psi_i\right)$ is a graph given by the algorithm $A(i)$. The incidence function ψ provides structure to a graph by associating to each edge an unordered pair of vertices in the graph as $\psi(e) = \left\{v_i, v_j\right\} : v_i, v_j \in V, \quad \forall e \in E \subseteq [V]^2$. Here i is the temporal component by virtue of which a network can evolve as per the given algorithm A.

A network is thus an empirical object the underlying graphs for which can be either deterministic as completely determined by an algorithm or stochastic as obtained by modelling real world data. However, a graph is an algebraic object such that an unlabelled graph represents an isomorphism class of otherwise labelled graphs. We call a network as static network if the temporal component Λ consist of a single element i, otherwise the network is a dynamic network. For the purpose of our work in this paper, we define an ecological network as a network N in which V_λ is the set of habitat patches for the target species/population, and E_λ is the set of flows of ecological matter between two distinct habitat patches.

The seed dispersion of representative Himalayan moist temperate anemochorous plants viz. *Abies pindrow, Betula utilis* and *Taxus wallichiana* thus forms a dynamic ecological network $N = (V_\lambda, E_\lambda, \psi_\lambda, \Lambda)$ with Λ consisting of three periods over the years 1985, 1995 and 2005. Here the vertices of underlying graphs represent habitat patches of these species that are connected by edges whenever the distance between two habitat patches is less than three hundred meters. The reason for choosing this distance is because three hundred meters is considered the threshold up to which these wind dispersed (anemochory) species can disperse (Vittoz and Engler, 2007).

2. Study area

The study has been carried out in the Western Himalayan region of India constituting the states of Uttarakhand, Himachal Pradesh and Jammu and Kashmir. The study area lies between 28°43′N to 37°05′N latitude and 72°31′E to 81°03′E longitude. It has a total geographical area of 3,31,382 km^2 of which Himachal Pradesh, Jammu & Kashmir and Uttarakhand covers 55,673 km^2, 2,22,236 km^2 and 53,483 km^2 respectively. The altitude varies from foothills of Himalaya ca. 50 m through 5,500 m. The terrain is diverse and it includes plains, undulating hills and high mountains (Hajra and Rao, 1990). The average annual rainfall is about 1800 mm, 600–800 mm and 1550 mm in Himachal Pradesh, Jammu & Kashmir and Uttarakhand respectively. Temperature varies from sub-zero to 40 °C. The region witnesses alpine and temperate climate except in the plains where the climate is tropical. As per the State of Forest report (2011), the recorded forest area of Himachal Pradesh is 37,033 km^2 which is 66.52% of its geographical area. Reserve forests constitute 5.13%, Protected forests 89.46%, and unclassed forests 5.41% of the recorded forest area. About two thirds of the state's recorded forest area is under permanent snow, cold deserts or glacier which is not conducive for the growth of trees.

The recorded forest area of Jammu & Kashmir is 20,230 km^2 which is 9.1% of the geographical area. Reserve forests constitute 87.21%, protected forests 12.61% and unclassed forests 0.81% of the recorded forest area. The recorded forest area of Uttarakhand is 34.651 km2 which is 64.79% of its geographical area. Reserve forests constitute 71.11%, protected forests 28.52%, and unclassed forest 0.35% of the recorded forest area. The Himalayan moist temperate forests in these three states stretch across the landscape. The three tree species considered in the study viz. *Abies pindrow, Betula utilis* and *Taxus wallichiana* are some of the indicator species and most responsive to the different stresses of climate and anthropogenic pressure. The information on habitat, distribution and environmental preference of these three tree species is elaborated in Table 1.

These tree species belong to a group of naked seed-producing plants called gymnosperms. The species that belong to this group are usually wind pollinated and wind dispersed with small and light seeds. In general, seed production in gymnosperms is intermittent but a very large quantity of seeds are produced for dispersal by wind. Hence, anemochory is the predominant (possibly exclusive) mechanism of dispersion in the aforementioned target tree species.

Table 1
A description of habitat, distribution and environmental preferences of target floral species. These tree species disperse diaspores only by wind.

Species	Distribution	Habitat	Altitudinal range	Temperature	Aspect	Timing of seed production
Taxus wallichiana (Himalayan yew)	China (Yunnan and Sichuan), Tibet, Nepal, Bhutan, Pakistan, India (Arunachal Pradesh, Himachal Pradesh, Assam), Myanmar, and some parts of Viet Nam	Evergreen and Coniferous forests	1800–3000 m	16°–24 °C, but can tolerate 2°–32 °C	Sheltered sites on chalk in the south-east and on limestone in the north-west	August–December
Betula utilis (Bhoj patra/Himalayan birch)	Afghanistan (Nuristan and Safed Koh) and northern Pakistan in the west, along the Himalaya and through the western Chinese Heng Duan mountains in northwestern Yunnan and southeastern Yunnan in the south, to Sichuan, Hubei and east to Hebei province in northern China.	Temperate Forest	2500–4500 m	4°–14 °C	North facing	July–August
Abies pindrow (Himalayan Fir)	Afghanistan east to Nepal, and the Karakoram Range in Pakistan	Montane to Subalpine zones	2000–3300 m	16°–24 °C, but can tolerate 2°–32 °C	Northern aspects and in shady localities	September–October

3. Materials and methods

Land use and land cover (LULC) of the Indian part of Western Himalaya for 1985, 1995 and 2005, which includes the three states of Himachal Pradesh, Jammu Kashmir and Uttarakhand, was generated using multispectral satellite data (Landsat MSS, Landsat TM and IRS-LISS III) at 1: 50,000 using onscreen visual interpretation. The maps were verified for accuracy using field data as well as high resolution Google Earth images for all the three time periods. The forest patches were subsequently extracted from the LULC. Since for a viable population of the target species of Himalayan moist temperate forests, a minimum patch size required is around 5 ha, hence forest habitats with less than 5 ha area were removed for the analysis.

Using the vector files prepared for the LULC of three time periods, two ASCII files named vertex file and distance file were generated using an open source software Confer 2.5 for each of the years (1985, 1995 and 2005). These two ASCII files were the inputs for the network analysis as the vertex and distance file together gives an adjacency list for the three years, where vertices are forest patches and distance between them is given. While it is true that the proportion of diaspores of a plant species exceeding a predefined reference distance using a certain dispersal mode is strongly context specific, for example large anemochorous trees disperse better in windy weather as compared to stormy weather or unstable atmosphere producing updrafts, because of the fact that dispersion is lesser in forests as compared to grasslands and gets reduced on hillsides due to downdrafts produced by winds we can safely assume that a very large fraction of diaspores are dispersed within three hundred meters of the source (Tackenberg, 2003; Tackenberg et al., 2003). And thus two vertices are considered adjacent in the network if the distance between them is less than the threshold distance of three hundred meters.

3.1. Computation of network centrality

Centrality indices are to quantify the intuitive notion that some vertices are relatively important and more central than others in the given network. Let G be a weighted or unweighted, directed or undirected multigraph and let X represent the set of vertices or edges of G respectively. A real valued function s is called a structural index if and only if following condition is satisfied

$$\forall x \in X, : G \cong H \Rightarrow s_G(x) = s_H(\phi(x)), \tag{1}$$

where $s_G(x)$ denotes the value of *s(x)* in G (Brandes and Erlebach, 2005). A real valued function is called a centrality index if and only if the following conditions are satisfied

$$\forall x,\ y,\ z \in X,\ f(x) \le f(y)\ or\, f(y) \le f(x)$$

$$f(x) \le f(y)\ and\, f(y) \le f(z)\ then\, f(x) \le f(z)$$

$$f(x) \le f(y)\ and\, f(y) \le f(x)\ then\, f(y) = f(x) \tag{2}$$

that is f induces a total order on X. By this order we can say that $x \in X$ is at least as central as $y \in X$with respect to a given centrality c if $c(x) \ge c(y)$. Thus every centrality index is a structural index but every structural index need not be a centrality index. Several centrality indices have been proposed by researchers from various fields over time. Indices like degree centrality, betweenness centrality, closeness centrality, eigenvector centrality and subgraph centrality are discussed here as well as computed for our network.

The degree of a vertex u in a graph G is the number of edges incident on that vertex. The degree centrality of a vertex is given by

$$C_D(u) = d(u) \tag{3}$$

where *d(u)* is the degree of the given vertex (Newman, 2003a). It can be computed as marginal of adjacency matrix A

$$C_D(\mathrm{i}) = \Sigma_j A_{ij} x_j = (Ax)_i \tag{4}$$

where x is a vector with each entry as 1.

As per degree centrality a vertex is more central the more it is directly connected to other vertices. Thus degree centrality is understood as a measure of immediate influence in a network.

Eigenvector centrality preserves the idea that a vertex is central if either it has many adjacent vertices or it is adjacent to vertices that have many adjacent vertices (and hence are more central in the network) (Bonacich, 1987). An eigenvector of a linear transformation is a non-zero vector whose direction does not change upon the application of the linear transformation. If $T : V \rightarrow V$, where V is a vector space over a field F, is a linear transformation then $\nu \in V$ is an eigenvector of T if $T(\nu) = \lambda \nu$ for some scalar $\lambda \in F$ called the eigenvalue associated with the eigenvector ν. If the vector space V is finite dimensional the above mapping can be represented as $Av=\lambda v$, where A is the matrix representation of the linear transformation T.

To define eigenvector centrality we begin by an initial guess of centrality x, given by a linear combination of eigenvectors $v_i$of the adjacency matrix A, that can be improved further by repeatedly iterating as per the process $x'=Ax$. After t iterations the centrality is

$$x(t)=A^t\sum_i c_i v_i=\sum_i c_i\lambda_i v_i=\lambda_1{}^t\sum_i c_i\left[\frac{\lambda_i}{\lambda_1}\right]^t v_i \tag{5}$$

where λ_i is the eigenvalue corresponding to eigenvector v_i and λ_1 is the largest eigenvalue of adjacency matrix A. Since $\lambda_i/\lambda_1<1$ for all $i\neq 1$, in the limit of large t, the centrality we obtained is proportional to the largest eigenvector. We call this centrality as eigenvector centrality, given by the equation

$$Ax=\lambda_1 x \tag{6}$$

Betweenness centrality characterizes the importance of a vertex when information is passed through a given pair of vertices (Freeman, 1977). Betweenness centrality measures the number of times the information passes through a vertex k by a shortest path between vertices i and j. Let $\delta_{st}(v)$ denotes the fraction of shortest paths between vertices s and t that contains v such that $\delta_{st}(v)=\frac{\sigma_{st}(v)}{\sigma_{st}}$, where $\sigma_{st}$is the number of all shortest path between s and t. The betweenness centrality of a vertex is given by

$$C_B(v)=\Sigma_{s\neq t\neq v}\delta_{st}(v) \tag{7}$$

Closeness Centrality considers a vertex more central if the total sum of distance from the given vertex to all other vertices is minimum. The closeness centrality is given by

$$C_C(u)=\frac{1}{\sum_{v\in V}d(u,v)}. \tag{8}$$

The measure is useful in the applications where a vertex is ranked higher if the vertex is close to most other vertices in the network (in terms of geodesic distance).

A walk in a simple graph $G=\left(V_G,E_G,\psi_G\right)$ is a sequence of alternating vertices and edges (not necessarily distinct), v_0, e_1, v_1, ..., v_k where $v_i\in V_G$ are vertices and $e_i\in E_G$ are edges such that $\psi_G(e_i)=\left\{v_{i-1},v_i\right\}$ for $1\leq i\leq k$. A walk is called closed walk if the initial vertex in the sequence is identical to the final vertex. Subgraph centrality of a vertex is the weighted sum of closed walks of different lengths in a network starting and ending at the given vertex (Estrada and Rodrıguez-Velazquez, 2005). Subgraph centrality is given by the equation

$$C_S(i)=\sum_{k=0}^{\infty}\frac{\mu_k(i)}{k!} \tag{9}$$

where $\mu_k(i)$ is the closed walks of length k starting and ending on vertex i.

3.2. Identification of scale-free networks

A given quantity x is said to obey a power law if its probability distribution is given by

$$p(x)=Cx^{-\alpha} \tag{10}$$

where α is a constant parameter of distribution called the exponent or scaling parameter and C is constant of normalization (Clauset et al., 2009). In general few quantities obeys a power law for all values of x. Typically there is a parameter $x_{\min}$ above which the values of x follows a power law (Barabasi and Albert, 1999).

Power law distributions are of two distinct kind. Continuous distribution where the quantity of interest vary continuously and discrete distribution where the random variable takes only a discrete set of values, generally positive integers.

For the discrete case x takes a discrete set of values and the probability distribution of x has the form

$$p(x)=Pr(X=x)=Cx^{-\alpha} \tag{11}$$

The distribution is undefined for $x=0$ and thus there must be some $x_{\min}>0$ such that the distribution does not diverges for the values of x above $x_{\min}$. The constant of normalization can be found and the equation becomes

$$p(x)=\frac{x^{-\alpha}}{\zeta(\alpha,x_{\min})} \tag{12}$$

where

$$\zeta(\alpha,x_{\min})=\sum_{n=0}^{\infty}(n+x_{\min})^{-\alpha} \tag{13}$$

is the generalized zeta function.

We use maximum likelihood estimation to give an estimate to the value of α. For discrete case MLE is given by the solution of equations with $x_{\min}>1$ as

$$\frac{\zeta'(\alpha,x_{\min})}{\zeta(\alpha,x_{\min})}=-\frac{1}{n}\sum_{i=1}^{n}lnx_i \tag{14}$$

In discrete probability distribution case discussed above we assumed that the value of $x_{\min}$ is given. However when $x_{\min}$ is not given, it can be estimated empirically by choosing an estimate that makes the cumulative probability distribution $S(x)$ and the best-fit power law model as similar as possible. The Kolmogorov – Smirnov statistic between two probability distribution is

$$D=\max_{x\geq x_{\min}}|S(x)-P(x)| \tag{15}$$

where $P(x)$ is the CDF for the power law model that best fits the data in region $x\geq x_{\min}$.

It must be noted that for a power law distribution if we take logarithm on both sides the Eq. (8) becomes

$$\ln p(x)=-\alpha\ln(x)+\ln(C) \tag{16}$$

Thus the most common way to establish that given empirical data has power law or not is by plotting the data on a doubly logarithmic scale and observing if the data follows a straight line or not. For a network the degree sequence of the underlying graph is plotted on a doubly logarithmic scale. If the values of the distribution indeed comes from a power law then the double logarithmic plot will be a straight line.

3.3. Identification of small-world networks

Clustering coefficient of a vertex in a network is the ratio of number of edges present among the adjacent vertices of the vertex and total number of edges possible among the adjacent vertices. Let $G=(V,E)$ be a graph. The clustering coefficient of a vertex u with set of adjacent vertices N_u is given by

$$C(u)=\frac{2|e_{ij}:i,j\in N_u,e_{ij}\in E|}{k(k-1)} \tag{17}$$

Where k is the number of vertices in N_u.

A similar idea is that of transitivity which is the ratio of three times the number of triangles present in a graph and number of connected triplets (L-shaped formations) of vertices in the graph (Newman, 2003a). Transitivity is defined as

$$T = \frac{3 \times number\ of\ triangles}{number\ of\ paths\ of\ length\ 2} \quad (18)$$

A network is said to possess small-world property if any vertex in the network can be reached by any other vertex in the network by traversing a path consisting of only a small number of vertices. It is observed that for a network G of order n and size m, the average shortest distance ASD is similar to an Erdos – Rényi random graph of same size and order. But the transitivity T_G and clustering coefficient C_G of the network is much higher than that for the Erdos – Rényi random graph T_{ER} and C_{ER} (Watts and Strogatz, 1998). This property is used to define a measure of small-world property. We call this as *small-world-ness* (Humphries and Gurney, 2008), which is defined as

$$SW = \frac{T_G \times L_{ER}}{L_G \times T_{ER}} \quad (19)$$

where L_G and L_{ER} are average shortest path length for the given network G and Erdos – Rényi random graph of same size and order. We call a network to be small-world if the value of small-world-ness is greater than one.

3.4. Assortative mixing

A network is said to show assortative mixing if vertices of higher degree are connected to vertices of higher degree and the vertices of lower degree tend to connect to vertices of lower degree. A network is called disassortative if the high degree vertices are connected to vertices of low degree. A measure for assortative mixing has been proposed (Newman, 2002). In a graph with Nvertices and M edges suppose we choose an edge e and arrive at a vertex v along the chosen edge e. Then the distribution of the remaining degree (the number of edges leaving the vertex other than the one along which one arrived) is given by

$$q_k = \frac{(k+1)\,p_{k+1}}{\Sigma_j j p_j} \quad (20)$$

where $p_k$is the probability that a vertex chosen at random in a network has degree equal to k.

Let e_{jk} be the joint probability distribution of the remaining degrees of the two vertices at either end of a randomly chosen edge. Then the assortative mixing (r) is given by

$$r = \frac{1}{\sigma_q^2} \Sigma_{jk} \left(e_{jk} - q_j q_k\right) \quad (21)$$

where $\sigma_q^2 = \Sigma_k k^2 q_k - [\Sigma_k k q_k]^2$ is the variation of q_k.

For the purpose of computations, assortative mixing is calculated as

$$r = \frac{M^{-1}\Sigma_i j_i k_i - [M^{-1}\Sigma_i \frac{1}{2}(j_i + k_i)]^2}{M^{-1}\Sigma_i \frac{1}{2}\left(j_i^2 + k_i^2\right) - [M^{-1}\Sigma_i \frac{1}{2}(j_i + k_i)]^2} \quad (22)$$

where j_i and k_i are the degrees of the vertices at the end of the ith edge where $i = 1 \ldots M$.

3.5. Communities in networks

Communities in a network are set of vertices that are present such that they have more edges linking the vertices within the set as compared to vertices outside of the set. Which means that the set forms a local cluster and has a locally cliquish topology. An arbitrary partition of the vertex set of a graph is said to form a good community structure if the value of modularity associated with it is close to one. Modularity as a measure was first proposed by Newman and Girvan in their seminal work on community detection (Newman and Girvan, 2003). A partition of a network into k communities can be represented by a $k \times k$ symmetric matrix E whose element $E_{ij}$is the fraction of all the edges connecting vertices in community i with vertices in community j. Given such a matrix E, modularity is defined as

$$Q = \sum_i (E_{ii} - a_i^2) = Tr(E) - ||E^2|| \quad (23)$$

where $a_i = \sum_j E_{ij}$ represent the fraction of edges with one end in community i, $Tr(E)$ is trace of matrix E and $||A||$ is the sum of elements of matrix A. Clearly, the maximum value possible for Q for any partition is one. Newman further proposed a fast greedy algorithm for community detection which starts with considering each vertex as a community and iteratively merges two communities such that a maximum level of increase in the value of modularity is achieved on merging the two communities (Newman, 2003b).

4. Results

The distribution of the natural forest patches in the western Himalaya of India is given in Fig. 1. The areas in green are the natural areas which can harbour the populations of the target species in the region. The patches of the natural areas suitable for the target species were considered for the analysis.

We extracted and studied networks for the seed dispersion network of the mentioned anemochory species of Himalayan moist temperate forests of Western Himalayas. The networks for the observed years 1985, 1995 and 2005 vary in size and order where the number of vertices represent the total number of patches present during the given period. The underlying graph of seed dispersal network for the year 1985 is formed of 2819 vertices and 3304 edges. The number of connected components are found to be equal to 546 of which 413 are isolated vertices with no edges. The giant component consists of 1600 vertices while the second largest component is of size 256 vertices.

For the year 1995 the network consists of 2909 vertices and 3386 edges and a total of 559 connected components out of which 420 are isolated vertices or habitat patches which are not close enough to other habitat patches such that ecological information (seeds) can flow from one patch to another. Again a threshold of three hundred meters is used to determine if ecological information can pass between habitat patches or not. The largest component is a giant component consisting of 1920 vertices.

The network for the year 2005 contains a total of 3576 vertices and 4678 edges. The network has a total of 610 components out of which 447 vertices are isolated vertices i.e. components of size one. Thus a total of 163 components contains at least one edge. The biggest component is a giant component having an order of 1905 vertices and the second largest component consists of 404 vertices.

We further computed centralities for the network and identified the most central forest patches. We list below as Tables 2 , 4 and 6 the top ten patches (vertices), as ranked by the five computed centralities for the years 1985, 1995 and 2005 respectively. Furthermore, we list below in Tables 3 , 5 and 7 the descriptive statistics of the centrality indices i.e. maximum and minimum value, mean, median, variance, standard deviation and standard error of the mean for the years 1985, 1995 and 2005 respectively.

The corresponding spatial location of these highest rank patches are shown in the maps given in Figs. 2–4:

We calculated assortativity for seed dispersal network and found the value to be −0.1146, −0.1417 and −0.1073 for the graphs of the year 2005, 1995 and 1985 respectively. A negative value of assortitative mixing across the graphs indicate that in seed dis-

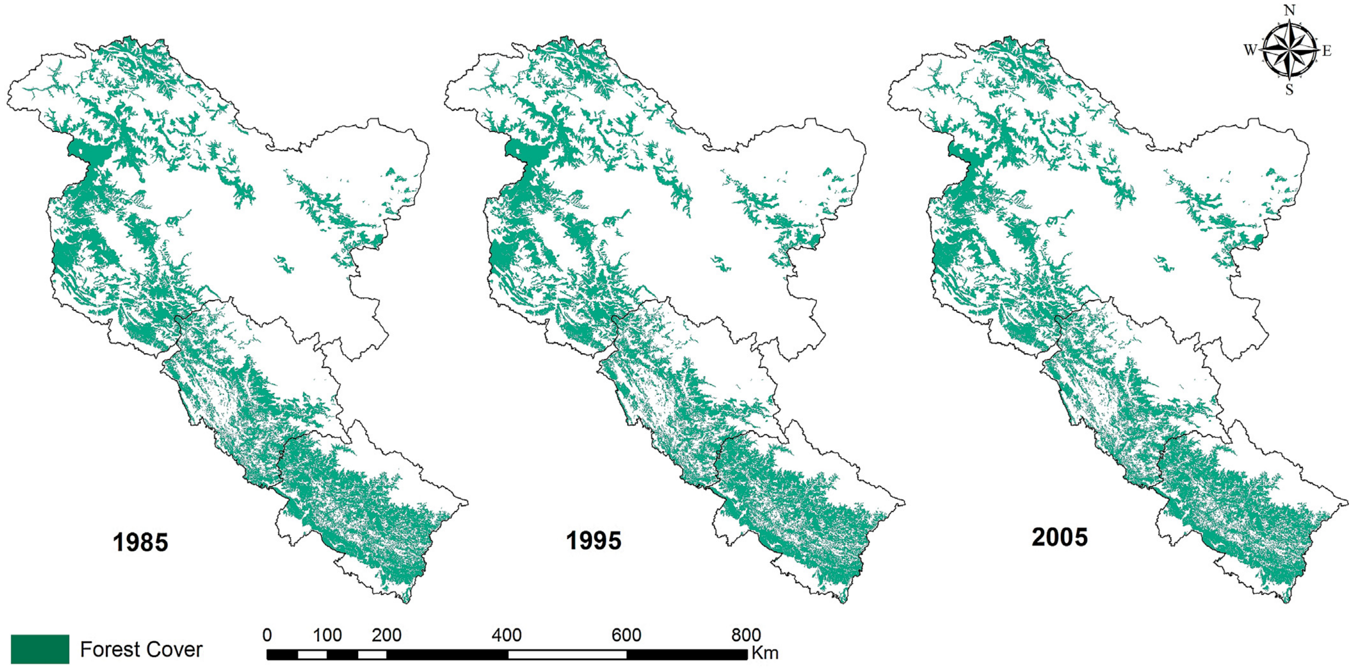

Fig. 1. Potential distribution of forest patches in the Western Himalaya region.

Table 2
Top ten central forest patches as ranked by various centrality indices for the year 1985.

Degree Centrality (C_D)		Eigenvector Centrality (C_E)		Betweenness Centrality (C_B)		Subgraph Centrality (C_S)		Closeness Centrality (C_C)	
Vertex No.	Degree	Vertex No.	Value	Vertex No.	Value	Vertex No.	Value	Vertex No.	Value
1811	200	1811	0.6808	1811	1.72E+06	1811	1.51E+06	1811	536.39
1572	106	2339	0.0803	484	1.05E+06	1572	2.54E+04	1572	460.15
1801	66	1694	0.0761	1572	1.05E+06	1694	2.16E+04	1694	456.53
598	61	2238	0.0720	1694	9.93E+05	2339	2.14E+04	1813	408.68
1309	61	2172	0.0686	1813	9.70E+05	2238	1.71E+04	1552	398.62
1694	57	2241	0.0677	443	8.98E+05	2172	1.54E+04	1561	393.85
778	50	2288	0.0671	598	5.42E+05	2241	1.50E+04	351	390.94
830	40	1737	0.0667	1788	4.64E+05	2288	1.47E+04	1702	390.94
1484	35	1735	0.0655	2356	3.67E+05	1737	1.47E+04	2339	388.36
484	34	1813	0.0654	1769	3.65E+05	1813	1.41E+04	1737	382.70

Table 3
Descriptive Statistics for the year 1985.

Centrality Index	Maximum Value	Minimum Value	Mean ($\bar{x}$)	Median	Variance (s^2)	Standard Deviation (s)	Standard error of the mean ($s/\sqrt{n}$)
C_D	200	0	2.3440	2	30.5494	5.5271	0.1041
C_E	0.6808	4.07E-20	0.0043	2.89E-10	3.36E-04	0.0183	3.45E-04
C_B	1.73E+06	0	6.86E+03	0	3.61E+04	6.00E+04	1.13E+03
C_S	1.52E+06	1.0000	1.19E+03	4.2033	8.21E+08	2.86E+04	539.7783
C_C	536.3962	0	148.7240	170.4048	1.73E+04	131.6291	2.4791

Table 4
Top ten central forest patches as ranked by various centrality indices for the year 1995.

Degree Centrality (C_D)		Eigenvector Centrality (C_E)		Betweenness Centrality (C_B)		Subgraph Centrality (C_S)		Closeness Centrality (C_C)	
Vertex No.	Degree	Vertex No.	Value	Vertex No.	Value	Vertex No.	Value	Vertex No.	Value
1632	106	1909	0.530	1909	2.18E+06	1909	3.29E+04	1909	489.41
1909	105	1754	0.405	562	1.87E+06	1754	2.53E+04	1632	466.52
1754	98	1773	0.136	1911	1.67E+06	1632	2.50E+04	1773	453.96
853	62	1632	0.126	684	1.43E+06	1773	4.30E+03	1754	449.72
684	61	2333	0.117	1632	1.35E+06	1369	2.49E+03	1911	404.58
1369	61	2331	0.092	1773	1.33E+06	853	2.12E+03	1621	391.29
1880	59	1714	0.092	2575	1.30E+06	1880	2.02E+03	2333	390.55
1773	57	2407	0.088	853	1.10E+06	684	1.67E+03	424	383.80
929	40	1795	0.082	1754	1.06E+06	2333	1.45E+03	1782	383.80
1544	35	1911	0.075	894	8.31E+05	2407	1.18E+03	1612	383.74

Table 5
Descriptive Statistics for the year 1995.

Centrality Index	Maximum Value	Minimum Value	Mean ($\bar{x}$)	Median	Variance (s^2)	Standard Deviation (s)	Standard error of the mean ($s/\sqrt{n}$)
C_D	106	0	2.3279	2	22.9350	4.7890	0.0887
C_E	0.5304	1.24E-20	0.0049	1.49E-09	3.19E-04	0.0178	3.31E-04
C_B	2.18E+06	0	1.30E+04	0	9.69E+09	9.84E+04	1.82E+03
C_S	3.29E+04	1.0000	75.1740	3.9692	8.30E+05	911.3297	16.8967
C_C	489.4174	0	159.8424	175.8182	1.62E+04	127.3172	2.3605

Table 6
Top ten central forest patches as ranked by various centrality indices for the year 2005.

Degree Centrality (C_D)		Eigenvector Centrality (C_E)		Betweenness Centrality (C_B)		Subgraph Centrality (C_S)		Closeness Centrality (C_C)	
Vertex No.	Degree	Vertex No.	Value	Vertex No.	Value	Vertex No.	Value	Vertex No.	Value
2218	106	2218	0.5705	2478	2.05E+06	2218	2.50E+04	2478	4.56E+02
2341	89	2478	0.2588	1253	1.93E+06	2341	1.53E+04	2218	4.55E+02
2478	86	2341	0.2143	2480	1.67E+06	2478	1.37E+04	2360	4.36E+02
1452	85	2360	0.2126	1122	1.51E+06	1452	8.77E+03	2341	4.26E+02
1955	61	2105	0.1126	1130	1.51E+06	2360	3.76E+03	2207	3.74E+02
2360	57	2007	0.0912	2218	1.33E+06	1955	2.49E+03	2049	3.74E+02
1625	54	2754	0.0829	2360	1.30E+06	1625	1.37E+03	2480	3.72E+02
532	41	2178	0.0794	1452	1.12E+06	2105	1.11E+03	2897	3.71E+02
2455	37	2191	0.0787	1241	9.99E+05	532	1.03E+03	2198	3.70E+02
2130	35	2630	0.0732	1030	9.73E+05	2897	899.275	2754	367.4525

Table 7
Descriptive Statistics for the year 2005.

Centrality Index	Maximum Value	Minimum Value	Mean ($\bar{x}$)	Median	Variance (s^2)	Standard Deviation (s)	Standard error of the mean ($s/\sqrt{n}$)
C_D	106	0	2.6163	2	18.9638	4.3547	0.0728
C_E	0.5705	1.65E-20	0.0040	9.89E-14	2.63E-04	0.0162	2.71E-04
C_B	2.04E+06	0	1.02E+04	0	7.44E+09	8.62E+04	1.44E+03
C_S	2.50E+04	1.0000	49.7440	4.6450	3.24E+05	569.9566	9.5311
C_C	455.8176	0	135.4046	144.6429	1.46E+04	120.8274	2.0205

persal network the higher degree vertices are mostly connected to vertices of low degree. Thus we infer the existence of patches that lie within the threshold distance of several other patches. However, patches that are close to several other patches are not close to each other. Disassortativity, as observed in our case, makes a network less robust in terms of connectivity (Rogier and Van Mieghem, 2015). Thus in case of failure of high degree vertices (extinction of high degree forest patches in the network) the network is likely to become disconnected.

We use maximum likelihood estimation as given by Eq. (14) to estimate the value of exponent α for the given network and found the estimated values to be equal to 3.13, 2.92 and 2.88 respectively for the networks of year 2005, 1995 and 1985. Also we found $x_{\min} = 4$ for the network of year 2005 and $x_{\min} = 3$ for other two networks as estimated by the method of Kolmogorov – Smirnov statistic given by equation (15).

The values of $x > x_{\min}$ and corresponding degree sequence of the underlying graphs for the given network was plotted on a doubly logarithmic scale as shown in Fig. 5.

The degree sequence as plotted on a doubly logarithmic scale for values of $x > x_{\min}$ follows a straight line in each case thus confirming that the seed dispersal network of given species of the Western Himalayas is a scale free network. Hubs in a scale-free network are the vertices with largest degree. For the network corresponding to year 2005, we calculated the degree share of hubs which is the ratio of degree of a vertex to total number of vertices in the network and found that the vertex with highest degree has 2.96% of degree share. Moreover the top ten highest degree vertices has an aggregate 18.2% of degree share.

A scale-free network with high clustering is said to show hierarchical organization and hence modularity if the clustering coefficient varies as the inverse of degree for a vertex as $C_G \propto \frac{1}{d}$, where d is the degree of vertex x (Ravasz and Barabasi, 2003). For the dispersal network corresponding to year 2005 we found no such scaling and the value of linear correlation coefficient between clustering coefficient and degree to be equal to 0.0778 thus indicating the absence of any linear correlation between the two quantities. This could be because the seed dispersal network shows geographical organization as this is one primary reason why hierarchical organization is not found in a scale-free network with high clustering as established by Barabasi and Ravasz (Ravasz and Barabasi, 2003).

We calculated average clustering coefficient C_G, transitivity T_G and average shortest distance ASD for the given networks of the year 1985, 1995 and 2005. We also compared these values with the average clustering coefficient C_{ER}, transitivity T_{ER} and average shortest distance ASD_{ER} of an Erdos – Rényi random network of same size and order. Thus we calculated small-world-ness SW for network of each year, as given by equation (19). The values obtained are summarized in Table 8. By observing the values of small-world-ness for the networks of year 1985, 1995 and 2005 we conclude that each of these networks possess the small-world property.

We used the fast algorithm by Newman to find communities present in the network and found that the networks for the year 1985, 1995 and 2005 contains a total of 160, 174 and 194 communities respectively. The value of modularity for the respective years is 0.9132, 0.9177 and 0.9350. The high values of modularity indicate a very prominent and well-formed community structure in the underlying graphs of the subsequent years. Moreover, if we compare the number of communities to the number of components present in the networks we conclude that there are some components which contain multiple communities. In terms of seed dispersal this could indicate that there exist patches which are closely knit such that there is mutual seed dispersion i.e. seeds from several neighbouring patches accumulate in every patch of the community because of denser connections between the members

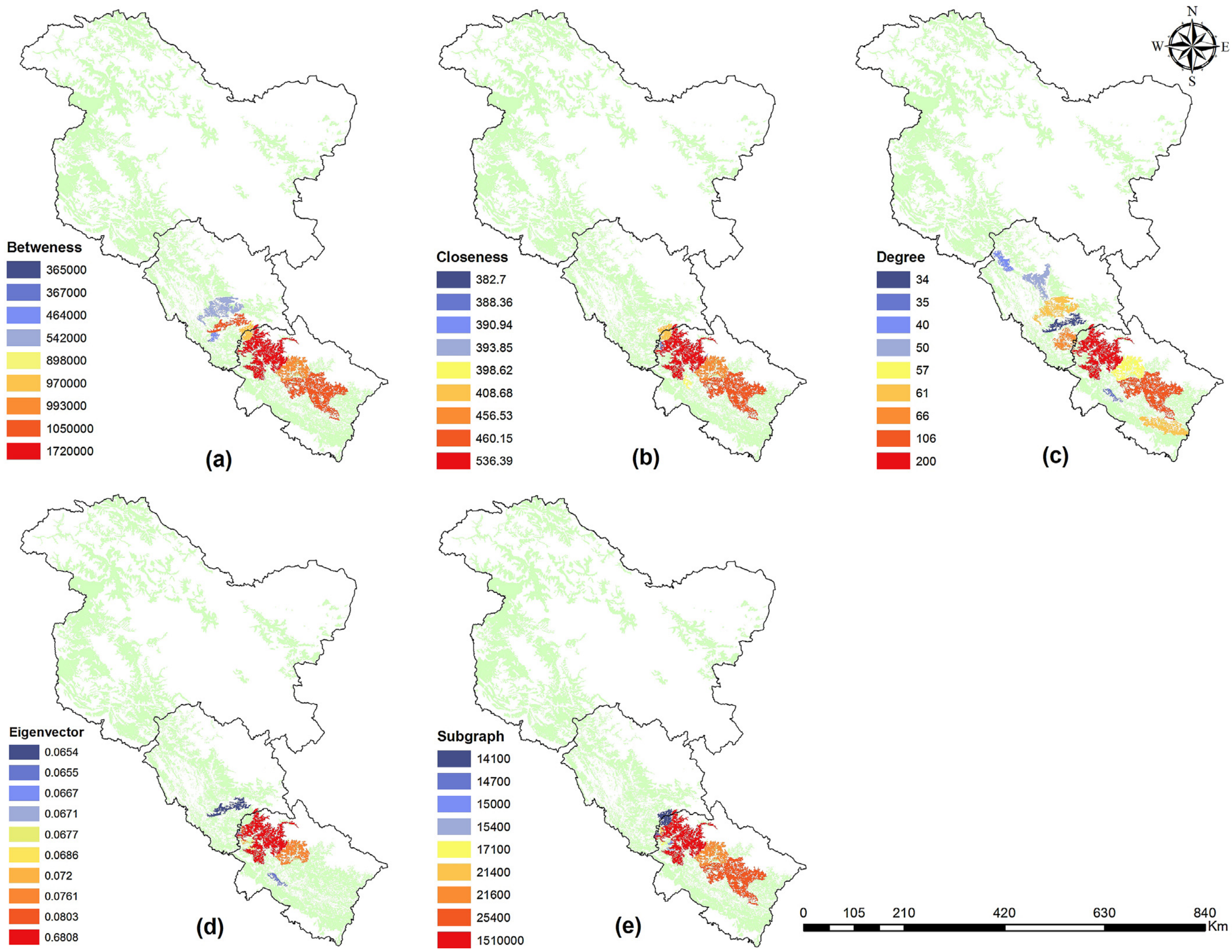

Fig. 2. Maps for various centrality indices computed for forest cover of 1985 for top ten patches. Most central patches as per (a) betweenness centrality, (b) closeness centrality, (c) degree centrality, (d) eigenvector centrality and (e) subgraph centrality are located here on map.

Table 8
Calculations for the small-world-ness of the given networks.

Network	C_G	T_G	ASD	C_{ER}	T_{ER}	ASD_{ER}	SW
1985	0.2766	0.0637	2.7654	4.19E-04	7.64E-04	6.7265	202.6398
1995	0.2698	0.0784	4.9153	4.81E-04	3.74E-04	6.5859	280.7912
2005	0.3220	0.1291	3.1500	0.0100	0.0017	6.7248	161.4958

of the communities as compared to patches outside of the community. In a given large component there are more than one location where such a phenomenon occurs.

5. Discussion

The forest patches that are best ranked according to different centrality measures are important for the purpose of conservation as they demand special consideration for the ecologically important role that they play in the process of anemochory of the target plant species in the Western Himalaya. The ecological roles played by these most central patches are diverse in nature and assigns a specific attribute and significance to the respective forest patch with respect to the process of seed dispersal in a region. For instance, the forest patches which are best ranked for degree centrality are precisely the hubs in the network. Also we observe that most patches are contiguous as indicated by the mean values of degree centrality of subsequent years.

It is observed that the forest patches which are not hubs but are top ranked according to the eigenvector centrality acts as relay points for passage of ecological information (seed dispersal) between hubs. This is particularly true for the given networks of the year 1985, 1995 and 2005 since we found that the hubs in these networks tend not to be connected as indicated by the negative values of assortativity. This is clearly instantiated in case of the networks of forest patches for subsequent years because the best ranked patches as per the eigenvector centrality lie in an area around Gangotri and a part of Yamunotri watershed. This area has very high relief and topography and is a relatively undisturbed area within the range of our study, due to the conservation status it enjoy. This area turns out to be a centre of dispersal of species between the Kumaon region and Himachal region which makes it a very important region in the event of ecological purturbation. In a similar way

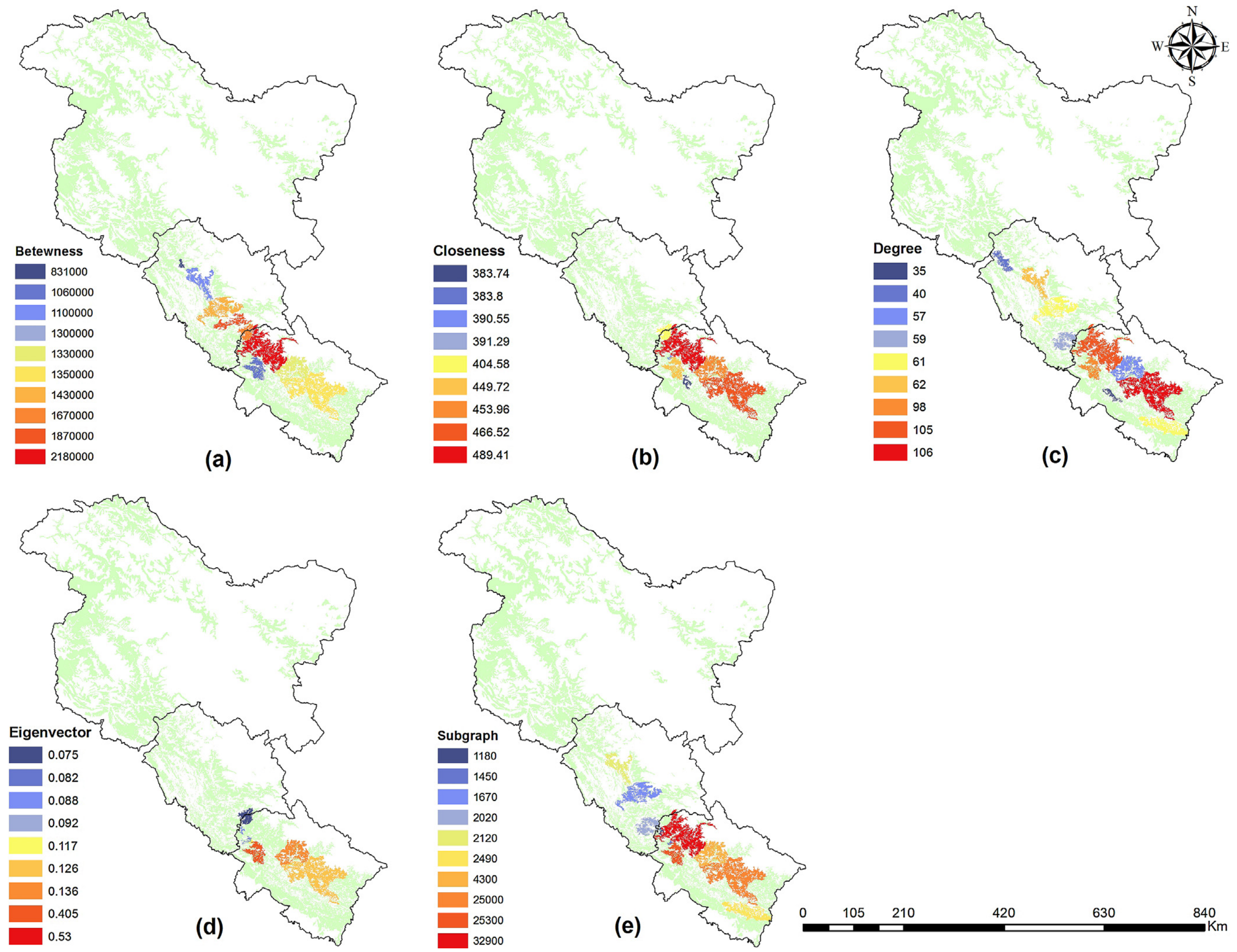

Fig. 3. Maps for various centrality indices computed for forest cover of 1995 for top ten patches. Most central patches as per (a) betweenness centrality, (b) closeness centrality, (c) degree centrality, (d) eigenvector centrality and (e) subgraph centrality are located here on map.

the patches which are best ranked as per the closeness centrality and betweenness centrality can be considered well placed in a network to facilitate the process of progressive propagation or spread of a plant species across the network. Such inference can be drawn because the best ranked forest patches here are either only a short distance away from most other patches in their component as in the case of closeness centrality or lies on shortest paths between several other forest patches in the component which is true for betweenness centrality. The forest patches for subsequent years which are best ranked by betweenness centrality lie in Central Himalayas ranging from the Kumaon region to Shimla region (up to Palampur) indicating that these patches may play an important role in species dispersion due to global warming. We further observe that a large number of forest patches do not lie on shortest paths between any pair of forest patches in the network, as indicated by the median value of betweenness centrality for subsequent years given in Tables 3, 5 and 7, respectively. The reason being that several different types of vertices in this network, for example, isolated vertices, pendant vertices, vertices of degree two that lie on a triangle, etc. do not lie on shortest paths between any pair of vertices and hence have a value of betweenness centrality as zero.

On plotting the forest cover we found that the forest patches which are best ranked according to different centrality measures occur mostly in the Gharwal region of the state of Uttarakhand and eastern Himachal Pradesh for all the three periods under discussion. Average temperature in this region ranges from -4° to 24° Celsius. The population density of these regions is lower as compared to the western side of Himachal Pradesh and Jammu and Kashmir. As a result these regions experience a minimum amount of anthropogenic pressure in terms of land use across the landscape and witness a maximum concentration of target floral species viz. *Abies pindrow*, *Betula utilis* and *Taxus wallichiana*. Forest fragmentation in this region is very low and most of the separation of the forest patches present in this region is due to the topographical features such as valleys, rivers and deep gorges. Any natural or anthropological disturbance in this region shall limit the flow of ecological information across the east – west ridge. This gives us an indication of the critical importance of the aforementioned geographical region to the dispersal and spread of the Himalayan moist temperate anemochorous floral species and thus forest patches in these regions must be conserved. An example of an important central forest patch present in this region was patch no. 1811 in the year 1985 that inherited the topographical features of this region and thus played critical role in propagation of ecological information.

The presence of hubs in our networks implies that a large number of vertices are incident to only a few vertices with high degree which is typical of a scale-free network. For the network of habitat patches this would mean that there is a very less possibility of the random extinction of plant species in a hub patch as there are many

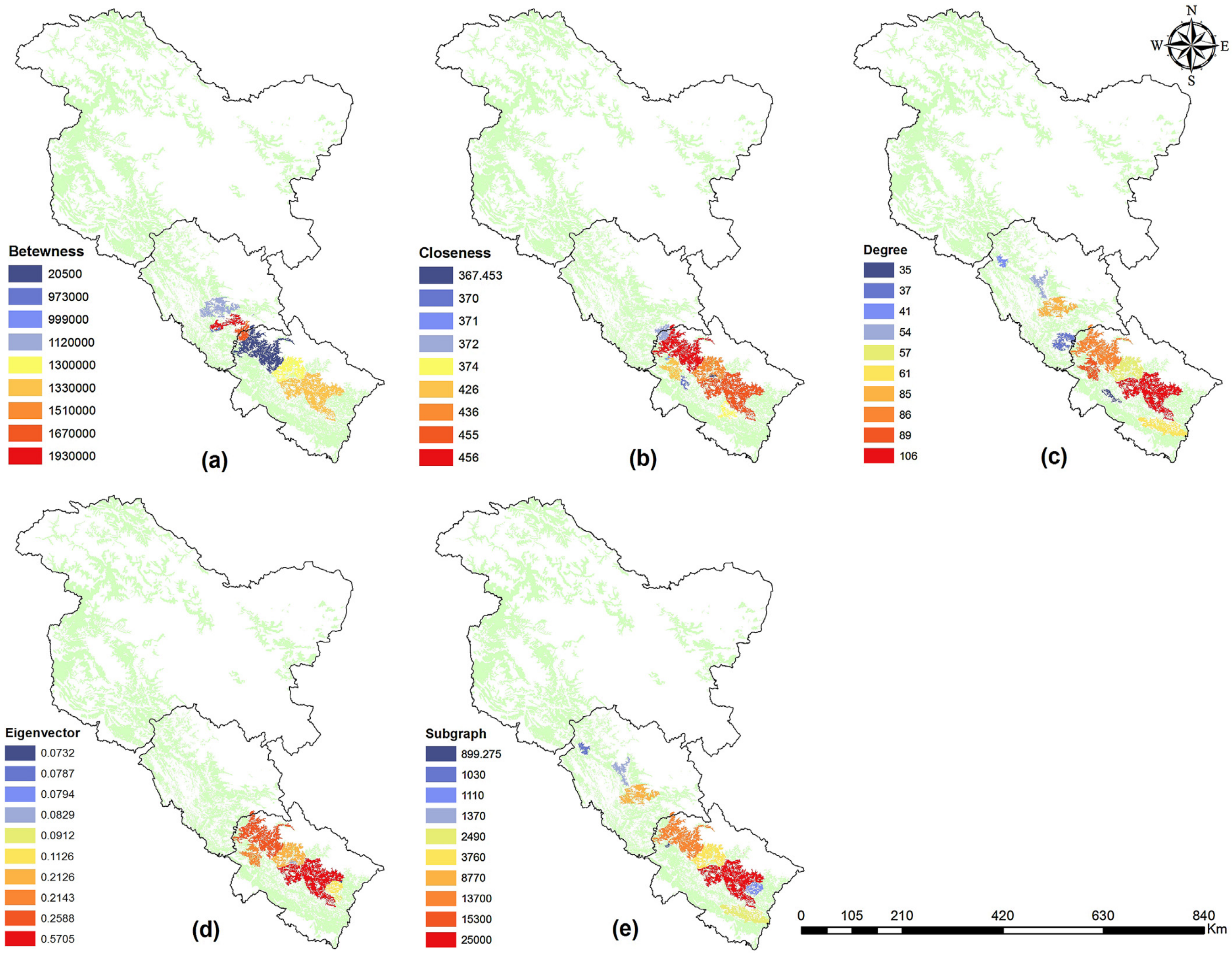

Fig. 4. Maps for various centrality indices computed for forest cover of 2005 for top ten patches. Most central patches as per (a) betweenness centrality, (b) closeness centrality, (c) degree centrality, (d) eigenvector centrality and (e) subgraph centrality are located here on map.

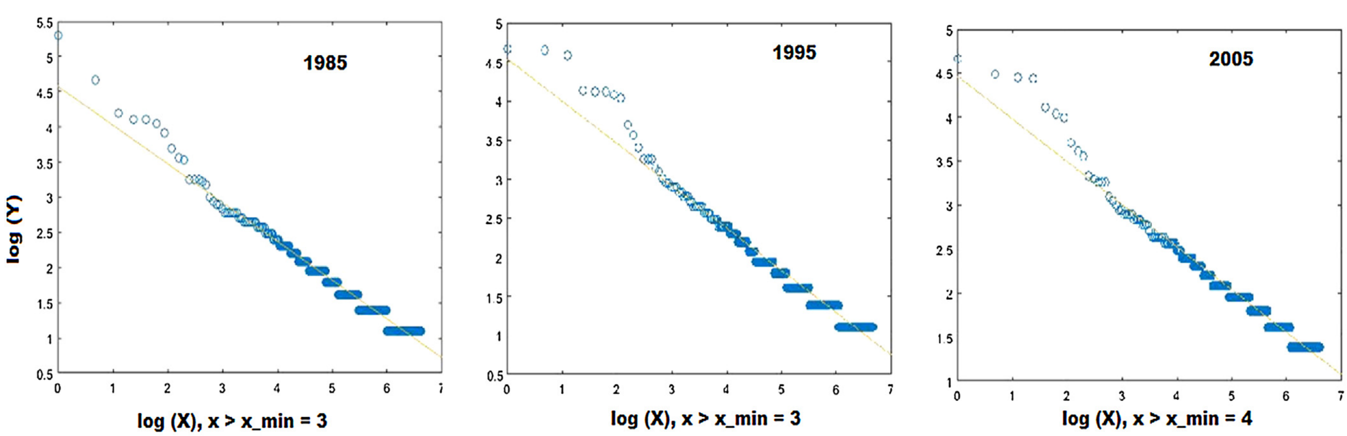

Fig. 5. Plot of degree sequence on a doubly logarithmic scale is found to be a straight line for each year thus confirming that the ecological networks are scale-free networks.

patches with a few patches or no patches close to them (Albert et al., 2000). It would also mean that once the plant species thrives in a hub patch it could further spread from there to patches adjacent to hub patch by dispersal and thus thrive in a large region.

The network being small-world implies that perhaps even being sparsely connected, there is high clustering at the local scale together with short average path length. For the process of seed dispersal this would mean that seeds from a forest patch in which the anemochory plant species are evenly present will disperse to neighbouring patches and since the neighbouring patches are themselves neighbours (presence of triangles in the network) the propagation of gene pool will take place evenly on a local scale.

As a consequence of the small-world property, an interesting network dynamics unfolds in the scenario when the species are introduced in a connected component of the network. Due to clustering the species when introduced to a forest patch will showcase an even spread locally in the forest component. The reason being that locally there is mutual dispersion from among the members of a cluster. Also, due to low average shortest path length in the network the spread of plant species becomes possible to relatively distant patches in the component as all the patches are only some steps away from each other. Thus due to mesoscale transitions the spread of species happens rapidly in a component on an ecological time scale. Moreover if a hub is present in the component then there is a sudden burst in the spread of the species when the species conquers a hub patch and begin dispersion from there. Thus the species when introduced to a connected component is likely to thrive because of scale-free and small-world nature of the network.

High clustering, as observed in the networks of subsequent years, reflects a locally high density of edges. This enhances the efficiency of communicating ecological information. Thus in a likely event of extinction of a plant species form a forest patch, possibly caused by a pest or viral infection, an efficient recolonization of the plant species in the patch is expected due to small world property of the network. Though it would also lead to a rapid propagation of undesirable ecological signal and perturbation i.e. such a pest or viral infection shall rapidly spread throughout the network component. A legitimate strategy for conservation in case of such an infectious outbreak across the network is to immunize and secure the hubs of the network as it increase the chances of eradicating the malicious agent (Dezso and Barabasi, 2002).

We further observe that the network of forest patch connectivity in the Western Himalaya region does not enjoy a high redundancy of links, thereby making it less resilient under the loss of links in the network. This lack of resilience in the network is also reflected from the average values of degree which for the network of forest patches lie in the range of 2.3–2.7 for all the subsequent years. The presence of communities and high transitivity in the network add to resilience and help mitigate this problem to some extent. However the effective resilience of network is boosted by the high degree of heterogeneity induced in the network by the presence of hubs (Gao et al., 2016). Thus the forest patches situated in the Western Himalaya region prevail to form a robust networked system.

6. Conclusion

Graph based network theoretic modelling helps in identification of the critical areas of connectivity given by various centrality indices, as well as the regions where the network is well established. These most central forest patches play specialized roles in the dynamics of flow of ecological information. This information will provide the managers and the ecologists a crucial scientific base to initiate conservation and mitigation measures at landscape level for maintenance of the ecological flow of information and matter. An example of such critically important forest patches are the hubs in the network which we conclude are resilient towards random extinction because of the network of forest patches being a scale free network. Based on the interpretation of results of centrality indices along with their descriptive statistics and by plotting the most central forest patches on map we conclude that forest patches which range from Uttarakhand to central parts of Himachal Pradesh are important for species movement. However many of the critical patches have suffered degradation over the subsequent years.

Connections in the network of forest patches are locally dense due to high clustering observed as a result of small-world nature of the networks and presence of communities. We thus conclude that ecological information propagate rapidly and evenly on a local level in the network of forest patches due to small-world property in the network. While on one hand it indicates that recolonization would be a success even within a relatively shorter period of time, on the other the small-world topology implies that malevolent signals like infections can potentially spread rapidly throughout the population. As a result an imperative management of hubs is proposed to support viable ecological functioning. Thus while the networks of forest patch connectivity in the Western Himalaya region showcase a tendency towards rapid transfer of ecological information due to small world property, they at the same time are robust and resilient by virtue of being a scale free network.

These results reflects a need for versatile efforts towards conservation in the light of the fact that removal of some of the critical patches may result in conversion of this scale free network into a scale dependent network and hence result in isolation of the populations and prevent exchange of genetic information among the population. This may also hinder flow of ecological information due to probable climate change and result in local extinction of the species. We are currently investigating this factor of loss of ecological information (leaks) as this process governed by several factors forms an important area for our further studies.

Finally, we speculate that in cases where dispersion mechanism is not exclusively anemochory, mode-specific dispersions (say, zoochory) shall determine specific dispersal distances of a potential source and hence may have an impact on the topology of the networked system. The principles of flow of ecological information shall apply to these networks in much the same way as they apply in our case if they showcase the same structural properties. Thus networked system lying in diverse habitats shall exhibit a similar pattern of wind dispersion of diaspores if their topological and structural aspects are same as found in the network of forest patches in Western Himalaya region studied here. However, differences in structural patterns and global properties of such networked systems may lead to discrete dynamics open for ecological interpretation and may create further avenues for contemporary research.

Acknowledgement

The authors AR, MR and ASK acknowledge the funding received from the Department of Space, Government of India, which has funded the generation of the database.

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