Linking dendritic network structures to population demogenetics:
The downside of connectivity

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Spatial structures strongly influence ecological processes. Connectivity is known to positively influence metapopulation demography and genetics by increasing the rescue effect and thus favoring individual and gene flow between populations. This result has not been tested in the special case of dendritic networks, which encompass stream and cave ecosystem for instance. We propose a first approach using an individual based model to explore the population demography and genetics in various dendritic networks. To do so, we first generate a large number of different networks, and we analyze the relationship between their hydrographical characteristics and connectivity. We show that connectivity mean and variance of connectivity are strongly correlated in dendritic networks. Connectivity segregates two types of networks: Hortonian and non-Hortonian networks. We then simulate the population dynamics for a simple life cycle in each of the generated networks, and we analyze persistence time as well as populations structure at quasi-stationary state. Our main results show that connectivity in dendritic networks can promote local extinction and genetic isolation by distance at low dispersal and diminish the size of the metapopulation at high dispersal. We discuss these unexpected findings in the light of connectivity spatial distribution in dendritic networks in the case of our model.

The study of spatial structures and their influence on population dynamics is one of the most challenging and active domains of ecology and evolution. Infinite island (Wright 1931, 1951), mainland-island (McArthur and Wilson 1967) and metapopulation (Levins 1970) models have greatly improved our understanding of population demography and genetics. More recent developments in population demography (Hanski and Gilpin 1997, Tilman and Kareiva 1997, Bascompte and Solé 1998) and genetics (Harrison and Hastings 1996, Rouset 2000) have brought these concepts to application through the study of dispersal, gene flow and connectivity (Cloquet et al. 2001, Moilanen and Hanski 2001). Although there is a trend to model more and more precisely the effect of habitat matrix on population dynamics (emergence of landscape ecology, Turner and Gardner 1991, Manel et al. 2003), some spatial structures have been relatively ignored until recently. This is the case of dendritic networks, as pointed out by Campbell Grant et al. (2007). Riverine and cave ecosystems are typical examples of dendritic networks that share contrasting features compared to classical terrestrial ecosystems. Their shapes vary greatly in complexity, and while it is obvious that ramification makes them not one-dimensional, they cannot be considered as two-dimensional (Tarboton 1996, Campbell Grant et al. 2007, Retho et al. 2007). Therefore, in dendritic networks, at least for most aquatic species, there is only one path to travel from one place to another. As a consequence, the distances between pairs of patches (i.e. river segments) of favorable habitat distributed along a dendritic network are not independent, unlike in most metapopulation models. Finally, migration between two patches not only affects departure and arrival patches demographically and genetically as in classical spatial models, but it may also affect intermediate patches. For these reasons, and also because these ecosystems are biodiversity reservoirs under strong anthropogenic pressure (Meffe and Caroll 1994), we believe it is of importance to relate networks geometry and connectivity variations to population dynamics and evolutionary outcomes.

Regarding the dynamics of meta-communities, recent studies outlined the importance of accounting for network spatial structures to understand patterns in evolution (Economo and Keitt 2007, Muneepeerakul et al. 2007). However, regarding population dynamics and genetics, many recent studies of riverine populations do not account for dendritic network topology (Matsubara et al. 2001, Meldgaard et al. 2003, Taylor et al. 2003, Neville et al. 2004, Jager 2006), and usually space is addressed as a linear structure (Speirs and Gurney 2001, Pachepsky et al. 2005, Labonne and Gaudin 2006). Implicitly, it is assumed that two-dimensional metapopulation concepts and results (sensu Hanski 1999) apply to the case of riverine systems. Yet the concern for the role of dendritic networks on population dynamics is growing: Schick and Lindley (2007)
developed an original approach using the mathematical graph theory to investigate connectivity between salmon populations. Charles et al. (2000) and Chaumot et al. (2006) modelled explicitly a dendritic river network for demography. By simulating population dynamics in symmetric and constantly bifurcating dendritic networks, Fagan (2002) clearly demonstrated that dendritic networks may produce demographic patterns very different from those expected from classical one-dimensional stepping-stone models, depending on dispersal mechanism. A mathematical approach relating population genetics and infinite dendritic networks was described by Sawyer (1978), but he did not investigate spatial variability in network structure, nor did he consider sexually reproducing organisms. Exploring the relationship between shapes of dendritic networks and population dynamics and genetics (i.e. demogenetics) is thus clearly needed. Because sufficient comparative data over a large range of networks are not available, such a question can be best handled using models.

In this study, we propose a preliminary approach to relate the structure of dendritic networks to population processes: we investigate a wide range of network structures in relation to organisms with a simple life cycle. To do so, we first randomly generate a large variety of dendritic networks, each composed of one hundred unitary river segments (or patches). We relate the structure of networks described by hydrographical descriptors to their intrinsic connectivity. Because connectivity is known to positively affect the metapopulation, we investigate the relationships between local connectivity and hydrographical descriptors. We then simulate simple population dynamics within these networks, using a stochastic individual-based model for sexually-reproducing organisms, accounting for dispersal, neutral genetics and density-dependence. We analyze the possible influence of networks connectivity on population viability and demogenetics at quasi-stationary state. Finally, we discuss the unexpected relationships between network structure, connectivity and population demogenetics in the specific case of our model.

Methods

Dendritic networks

Generation of networks

Artificial dendritic networks were generated using a stochastic branching process, coded as an extension on the CAPSIS-4 modeling platform (Goreaud et al. 2006, <http://coligny.free.fr>), using JAVA 1.5 language and algorithms. The network was built as an assemblage of units of favorable habitat (hereafter referred to patches) similar in length and carrying capacity. From a hydrological point of view, a patch may correspond to a river segment or branch, and in our case, all patches are favorable and contiguous (i.e. these segments are not separated by corridors or unfavorable habitats). In this model, nodes are considered as transfer points between patches (sensu Campbell Grant et al. 2007), but are not modelled as habitat. The generation process started from an initial downstream patch (the root of the dendritic network). At each node, the number of upstream patches, which could be either 0 or 1 or 2, was randomly generated using a probability triplet summing to one, constant through the generation process, and randomly chosen from a uniform distribution for each new network (Fig. 1). The generation process was repeated until the total number of patches reached 100. Networks presenting more complex branching (nodes presenting more than 2 upstream patches) were not generated, as they are infrequent in natural systems. Nodes with only one upstream patch produced a linear branch of length 2, leading to branch length variation at the scale of the final network. Because the generation process is stochastic, two networks generated with a same probability triplet can

![Figure 1. Examples of simple generated network under various probability triplets to lead the branching process. The total size of network is seven patches, the initial patch is shown in grey, and the probability triplet associated to each network is provided.](image-url)
differ, and inversely, different probability triplets may also happen to produce similar networks (Fig. 1).

**Fractal measures for network selection**

Dendritic river networks can be viewed as geometrical objects with intrinsic structural laws, stemming from the dynamics of their genesis (i.e. erosion caused by water flow on a given substrate). It has been shown that in natural networks, branch length and drainage area obey some statistical power laws and therefore exhibit fractal structures (Horton 1945, Strahler 1957, Mandelbrot 1983). This scaling has been used by hydrologists to propose synthetic theoretical descriptors of networks shapes (Abrahams 1984). Branches are usually classified using Strahler ordination: head streams are first order branches; when they join another branch of equivalent order, they form a new branch of superior order (Strahler 1957). Horton’s ratios are the commonly used descriptors of the degree of bifurcation and branch length distribution in a river network. At each order level \( \omega \) in a given network, the bifurcation ratio \( R_n(\omega) \) is calculated as follows:

\[
R_n(\omega) = \frac{n_{\omega-1}}{n_{\omega}}
\]

with \( n_{\omega} \) the number of branches of order \( \omega \). The branch length ratio \( R_l(\omega) \) is calculated as follows:

\[
R_l(\omega) = \frac{l_{\omega}}{l_{\omega-1}}
\]

with \( l_{\omega} \) the mean length of branches of order \( \omega \). According to Horton’s law, \( R_n(\omega) \) and \( R_l(\omega) \) should be constant across orders, so that the ratios \( R_n \) and \( R_l \) characteristic of a given network could be derived from their estimation at any order level. In practice however, there may be some deviations to Horton’s law. Here network estimates of \( R_n \) and \( R_l \) were chosen to be the slopes of the linear regressions between the order level and the number of branches or the mean length of branches in a log scale respectively (Dodds and Rothman 2001). The higher the bifurcation ratio \( R_n \), the higher the number of small-order branches compared to higher-order ones. The higher the branch length ratio \( R_l \), the longer the high-order branches in the network compared to low-order branches. The values of \( R_n \) and \( R_l \) have been estimated in a number of natural river networks and have been shown to vary between some “natural” limits (Abrahams 1984), namely \([3–5]\) for \( R_n \) and \([1.5–3]\) for \( R_l \). We therefore eliminated networks presenting unrealistic \( R_n \) or \( R_l \) values from our simulations. We sampled the final distribution of obtained networks in order to fully explore the most diverse combinations of \( R_n \) and \( R_l \) descriptors (being not necessarily typical of distributions observed in nature) and also to reduce simulation times. As a result, 208 among 1000 networks were retained for the analysis.

**Connectivity measure**

As an alternative to physical descriptors of network structure, dendritic networks may also be seen as networks of favorable habitat patches connected by migration, namely metapopulations. In a metapopulation, a major determinant of population dynamics and genetics is connectivity. In non-fragmented habitats, buffer measures of connectivity (i.e. number of occupied patches in a limited neighborhood as defined by Moilanen and Nieminen 2002) are suitable for demography. In addition, for fragmented habitats, size of habitat, and possibly immigration rates are important. However, in the present study, all patches present the same characteristics, and the distance between two contiguous patches is constant. We also wished to use a measure independent from demography. We therefore defined connectivity as the number of neighbor patch within a radius ranging from 1 to 5 patches (without counting the focal patch). Total network connectivity was estimated by the mean and variance of these five patch connectivity measures, hence generating 10 different measures.

**Population simulation model**

**Life cycle**

We considered a very simple life cycle, appropriate for species with average fecundity (0 to 5 offspring) and short life span representing a relatively fast population dynamics. Each female reproduced once per time step whatever her age, conditionally on male presence in the patch. A male was chosen at random. Fecundity was drawn from a Poisson distribution of parameter \( \mu \). Sex ratio was equilibrated at birth, and each individual survived with probability \( S \). Dispersal was designed as in a random-walk stepping-stone model: each individual could leave the patch with probability \( m \) with equal chances to move upstream or downstream to the nearest patch. In case of upstream migration through a confluence, individuals randomly settled in one of the upstream patches. Finally, each individual had a single diploid neutral locus, with five possible different alleles. Offspring inherit alleles from their parents through a classic sexual transmission.

**Simulation of population dynamics and genetics**

Population model was also coded on the CAPSIS-4 modeling platform (module dynet, code accessible on request). We used a discrete-time dynamic model, accounting for dispersal, demography, sex and neutral genetics between the hundred patches. In order to simulate both demography and genetics, we used an individual-based approach. The individual scale is appropriate for realistic demogenetic investigations, because individual behavior can be modeled at the same scale as genetic map, and because demographic stochasticity is an intrinsic propriety of the model (Grimm et al. 1999, DeAngelis and Mooij 2005). We introduced a constant carrying capacity for all patches to limit the size of the metapopulation. When local density exceeded 100 individuals per patch, individuals in excess were removed randomly – prior to reproduction. Consequently, the total metapopulation could at most contain 10 000 individuals.

**Simulation protocol**

As initial conditions, 100 individuals were introduced in each patch, with equal allelic frequencies and equilibrated sex-ratio. Various values of dispersal rate \( m \) were investigated; three of them are presented in this paper (\( m = [0.01, 1481

1481
In a first set of simulations, we analyzed the dynamics of global extinction. For obvious practical reasons, we ensured that all patches would go extinct before 5000 generations by adopting the following survival rate and mean fecundity: $S = 0.675$, $\mu = 1$. One hundred Monte Carlo trajectories were performed for each network and each dispersal rate and we recorded time until extinction for each trajectory. In a second set of simulations, we examined the dynamics at quasi-stationary equilibrium (i.e. quasi-stable distribution of metapopulation size and patch occupancy). Such state was obtained by using $S = 0.685$ and $\mu = 1$, for all dispersal rates. Twenty-five Monte Carlo trajectories of 5000 time steps were performed for each network and each dispersal rate. Only the final population structure is analyzed in this paper.

Descriptors of population demographic and genetic structure

We retained eight descriptors of population structure. Three of them were purely related to demography: total number of individuals in the network (metapopulation size), variance of patch density and local extinction probability (measured as the proportion of patch hosting less than five individuals). Four descriptors were meant to capture the distribution of genetic diversity in the metapopulation: the total number of alleles in the metapopulation (ranging from 1 to 5), the mean patch allelic diversity (also ranging from 1 to 5) and its variance over all patches, and the mean level of genetic differentiation between patches ($F_{ST}$, Wright 1951). Finally, the effect of distance on genetic structure was assessed through a genetic isolation-by-distance (IBD) indicator (estimated as the slope of the linear regression between the pairwise $F_{ST}/(1-F_{ST})$ ratios and patch distances, Rousset 1997).

To analyze the results, we fitted linear models between the measure of network connectivity and all dependent variables of interest (demogenetic descriptors). However, as explained below, because we found two different groups among the simulated networks (Hortonian versus non-Hortonian), we fitted three different models: 1) a simple linear regression between connectivity and the dependent variable, 2) a linear model (one-way Anova) accounting only for the group effect on the dependent variable, 3) a linear model accounting for both connectivity and group effect as well as their interaction on the dependent variable. These three models were labeled $M_c$, $M_h$ and $M_{c*h}$ respectively. Their respective quality of fit was assessed using the adjusted multiple correlation coefficient $R^2$. Because of the size of the data set (5200 observations), these coefficients were almost always very significant, so we relied on the percentage of explained variation rather than p-values to interpret our results.

Results

Generated networks

We finally retained 208 networks covering most of the $R_n - R_l$ space ($R_n$ ranging from 3 to 5, $R_l$ ranging from 1.5 to 3, Fig. 2). While some combinations were statistically difficult to obtain, the resulting distribution covered a variation range large enough to explore the role of network structure. We analyzed the mean and variance of the connectivity measures at the five different radius. All measures appeared strongly correlated over the generated networks of this study (normed principal component analysis, PCA, 92.45% of inertia on the first axis). In addition, the mean number of neighbors was highly correlated with its variance for each radius (the regression between mean and variance explains 78% to 91% of the total variance depending on the radius, see Fig. 3 for example). To simplify the subsequent analyses, we retained the variable that best represented the correlation among network connectivity variables (i.e. the highest weight on the PCA first axis): the mean number of neighbors within a 4-units distance (hereafter denoted $C$). It is important to
note that all subsequent results do not really depend on this initial choice: all different measures of connectivity tested behaved qualitatively and quantitatively the same way, with little variation in explained variation of patterns. We then explored the relationships between hydrological descriptors and C. No correlation was found between Rn and C, but the relationship between Rn and C showed a strong bimodal pattern (Fig. 4). Low Rn values were associated to low and high connectivity values, however, high Rn values were only associated to low connectivity values, and two groups were clearly distinguished. These two groups reflected two kinds of networks that will hereafter be addressed as Hortonian and non-Hortonian networks respectively (examples and description in Fig. 5). Hortonian networks present confluence between reaches of equal or consecutive orders, whereas non-Hortonian networks may present confluences between reaches of very different orders (Tokunaga 1978). One of the immediate consequences is that connectivity is not distributed similarly in the two types: Hortonian networks present a higher variance, illustrated by a skewed distribution with a longer tail (Fig. 5). We thus integrated this categorization in our analysis to retrieve analyze the role of connectivity in each type of network (hence models M_c, M_h and M_c×h).

Metapopulation persistence time and connectivity

Using the first set of parameters (declining populations), the model generated substantial variance in persistence time (mean = 796, min = 253, max = 3277), and the persistence time increased logically for higher dispersal values. The correlation (R^2) between persistence time and connectivity for the M_c model ranged from 0.002 for low dispersal (m = 0.01) to 0.05 for high dispersal (m = 0.20). The same range of correlation was obtained when considering the interactive M_c×h model, but it was a bit lower with the M_h model for high dispersal values (R^2 = 0.039 for m = 0.20). Hortonian networks presented the shortest persistence time, but the effect was weak. For instance under the M_{c×h} model, the predicted persistence time for a connectivity value of 11 was 1019 generations for Hortonian networks and 1048 generations for non-Hortonian networks. Connectivity had also a weak but negative effect on persistence time: the relationship between connectivity and persistence time was negative for both types of networks though a bit stronger in non-Hortonian networks. Looking at the dynamics in some simulations into details, we observed that patches located near branch tips (order 1) tended to go extinct first, but patches located near the root (order 4 to 5 usually in our simulations) were also quickly extinct. The last patches to go extinct were those located at intermediate positions (order 2 to 3).

Population demography and genetics at quasi-stationary state

For the second set of simulations, after 5000 generations, the model showed a quasi-stationary state, depending on the level of dispersal m. Explorations of population structure before 5000 generations showed that all simulations were already stabilized after 500 to 1000 generations. Average metapopulation size at the quasi-stationary state usually reached 8000 individuals, except for the lowest value of m, where it decreased to 6000 (Fig. 6a). As expected, metapopulation level of genetic differentiation (global F_{ST}) was influenced by dispersal, ranging from an average value of 0.1 for m = 0.20 to 0.7 for m = 0.01 (Fig. 6b). Genetic isolation by distance was also linked to dispersal, the largest mean values and variances being observed for m = 0.01 (Fig. 6c). Local extinctions, which in our model can be attributed to demographic stochasticity, were present at a significant rate only for m = 0.01, with 20% of extinct patches. This rate decreased below 1% for all other dispersal values. Allelic diversity at the metapopulation level was slightly and negatively influenced by dispersal (χ^2 test, p < 0.0001), but allelic diversity at the patch level was strongly and positively influenced by dispersal (one-way ANOVA, R^2 = 0.73). Calculating the local effective size sensu Wright (1931) under the infinite island model, we obtained a result of 7 individuals per patch, which was about one tenth of the average local density.

Relationships between network connectivity and demogenetics

Here we present the general effect of connectivity on population demogenetics (model M_{c×h} and only address the differences between Hortonian and non-Hortonian networks (models M_h and M_c×h) in the cases where correlation is sufficiently high.

We found consistent correlations between connectivity and demographic descriptors for all dispersal rates under the M_c model (Fig. 7). Metapopulation size was negatively correlated with C, whereas patch occupancy variance showed positive correlation with C. Correlation was clearly stronger for high dispersal rate (R^2 = 0.53 and 0.43
respectively) than for low dispersal rates ($R^2 = 0.08$ and 0.09 respectively). At low dispersal rate, where local extinction occurred frequently, local extinction probability was positively correlated with $C$ ($R^2 = 0.09$). These correlations were relatively independent from our Hortonian categorization except for high dispersal rates and high connectivity values, i.e. when overall correlation was high. An additive effect was found for metapopulation size ($R^2 = 0.57$ for $M_{c \times h}$ and $R^2 = 0.47$ for $M_h$ models), with Hortonian networks presenting a lower metapopulation size, whereas an interactive effect was found for patch occupancy variance: connectivity had a weaker effect on Hortonian networks for this descriptor.

Connectivity was not related to final allele number in the network (Poisson regression, percentage of explained variance = 0.01, 0.00 and 0.02 respectively for $m = 0.01$, 0.05 and 0.20). The mean number of allele per patch was also not related to $C$ ($R^2$ ranged from 0 to 0.02, Fig. 8). Variance of allele number was positively correlated with $C$ for low dispersal ($R^2 = 0.06$) but slightly and negatively influenced by $C$ for high dispersal ($R^2 = 0.02$). $F_{ST}$ distance was negatively correlated with $C$ in all cases (up to $R^2 = 0.054$ for $m = 0.20$). Finally, we found an important positive correlation between genetic isolation by distance and $C$ for low dispersal rates ($R^2 = 0.12$). For this relation, variance also tended to increase with the value of $C$. No noticeable effect of Hortonian categorization was detected for final allele number, mean or variance of allele number per patch. Such an effect was only consistent when correlation was higher. For instance, $F_{ST}$ measure decreased faster with connectivity in non-Hortonian networks. Hortonian networks tended to have a more important isolation by distance for high connectivity than non-Hortonian networks ($R^2 = 0.12$ for $M_{c \times h}$ model).

**Discussion**

In this first attempt to relate dendritic network shapes to population demogenetics, we found strong correlations between metapopulation size, extinction probability, genetic isolation by distance, and connectivity, as measured by
the number of neighbor patches within a given radius. We also found that deviation from Horton’s laws had a potential influence on population dynamics. We will first address the structural relationships between dendritic networks and connectivity in the simulated networks, then we will discuss the mechanisms and consequences of demogenetic variation linked to network structures in the case of the simple biological model chosen here. Finally, we will browse the various perspectives raised by this initial modelling approach.

**Generated networks**

In this study, we generated simple networks using a stochastic assemblage of unitary river segments, each corresponding to a habitat patch. The network generation method was randomized in order to avoid favoring a given arbitrary network shape. The range of simulated networks effectively induced consistent differences in population demogenetics. However, some shapes of natural networks may not be represented in the sampling. To overcome this possible bias in network sampling, one promising way to proceed would rely on the use of process-based models or more complete statistical models that are more likely to generate realistic networks (Rodriguez-Iturbe and Rinaldo 2001). For such realistic models and data structure, other descriptors are available (Gaucherel 2003) that could also be investigated in their relationships with population demogenetics. Another possible limit of our sampling is the limited number of patches in a network. For instance, preliminary analyses showed that bigger networks (300 patches) provide more homogeneous distribution between $R_n$ and $C$ without completely removing the bimodal trend (high values for $C$ implies low values for $R_n$, results not shown). The relatively small size of simulated networks may still correspond to a wide range of situations, where the distribution of favorable patches in the network is scarce, or when the watershed itself does not present orders higher than 4 or 5.

It is nevertheless remarkable that networks are distributed in two groups along a connectivity gradient. This finding provides an interesting insight on how hydrological structure and the chosen measure of connectivity are partially related. High values of the bifurcation ratio $R_n$ are only found for low connectivity values, and these networks do not follow Horton’s law of branching between consecutive orders (Tarboton 1996). In other words, given the size of the simulated networks in our study, these networks authorize connections between segments of order 1 or 2 with segments of order 4 to 5, which are located at the root of the network. This is well illustrated by the strong relation between mean and variance of connectivity: in non-Hortonian networks, connectivity is spread throughout the whole network, whereas for Hortonian networks, we observed an increased variance in connectivity: some patches are intensively connected with their neighbors, whereas some others are more isolated. Our guess is that connectivity is higher in the intermediate and upstream part of the network, thus generating spatial variation in connectivity: this possibility could be further investigated by using more complicated descriptors of networks spatial structure (Newman 2003). Such constraint between mean and variance of connectivity is usually not found in classic metapopulation model, because connectivity between patches is less constrained by the spatial organisation of landscape. Classifying networks on their Hortonian character is thus a first approach of connectivity, and it would

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Figure 6. Frequency diagram of (a) metapopulation size, (b) metapopulation $F_{ST}$ and (c) genetic isolation by distance for each value of dispersal rate $m$, after 5000 generations simulated.
be interesting to study the physical factors that provoke strong deviations from the Hortonian structure.

**Influence of connectivity measure**

In the present paper, we summarized our findings by presenting only one measure of connectivity (mean number of neighbors within a 4 distance units radius). Among the ten buffer measures of connectivity we explored (variance and mean of neighbors within 1 to 5 distance units), all measures provided the same qualitative patterns. They sometimes differed quantitatively in small proportions. Regarding persistence time, all connectivity measures performed equally (all correlations ranged from 0.047 to 0.053). Regarding dynamics at quasi-stationary state, using the mean number of direct neighbors (1 distance unit) increased the correlation from 0.12 to 0.14 between connectivity and genetic isolation by distance (for \( m = 0.01 \)), while accounting only for the mean number of direct neighbors (1 distance unit) decreased this correlation to 0.10. In the same way, at high dispersal rate (\( m = 0.20 \)), using the mean number of direct neighbors (1 distance unit) increased the correlation from 0.57 to 0.61. In some proportions, proximate connectivity appeared to be better suited for demographic predictions at high dispersal, whereas long distance measures were more efficient for genetic measures at low dispersal. Yet overall, relationships between connectivity and population demogenetics were rather independent from the scale of connectivity measures. However, this observation is restricted to the present results and should be explored further by varying the biological model.

In our measures of connectivity, we did not consider the population size of each neighbor patch, or the proportional immigration to the focal patch. These additional informations are included in some connectivity measures such as the incidence function models (IFM, Hanski 1999) acknowledged by Moilanen and Nieminen (2002). However, these types of measures are already related to population dynamics, whereas, as a first step, we wanted to relate

Figure 7. Plots of metapopulation size, patch occupancy variance and local extinction probability against network connectivity \( C \), for Hortonian (circles) and non-Hortonian networks (crosses). Relationships are provided for three dispersal rates (\( m = [0.01, 0.05, 0.20] \)) except for the local extinction probability, because significant extinction only occurred at low dispersal rate. The fit of the different models \( (M_c, M_h \text{ and } M_h/C) \) is measured by the multiple correlation coefficient \( R^2 \) (all \( p \)-values below 0.0001, \( n = 5200 \)). Only the predictions of the \( M_h/C \) linear model are represented, the full line shows the fit for Hortonian networks, the interrupted line shows the fit for non-Hortonian networks.
hydrological structures and connectivity as physical variables explaining the distribution of available habitat in the network. Yet in future works, other measures of connectivity could also be explored, especially to reflect local dynamics in networks. While IFM may be a good candidate to compare dendritic networks to classic metapopulations, other types of spatial measures linked to connectivity have been defined for networks in general. The degree of a patch generally describes the number of direct links towards other patches: this is equivalent in our case to the number of direct neighbors, but it could be different for species that are able to punctually perform out-of-the-network movements (riverine birds come to mind), or if one considers the state of neighbor patches (colonized or not for instance).

The distribution of this degree measure in a network is a powerful tool to characterize the overall network properties. To explore the sub-structure of the network, which is probably the next step to undertake to improve our insight.

Figure 8. Plots of mean allele number, variance of allele number, FST distance and genetic isolation by distance against network connectivity C for Hortonian (circles) and non-Hortonian networks (crosses). Relationships are provided for three dispersal rates (m = {0.01, 0.05, 0.20}). The fit of the different models (M_h, M_hc, and M_hc) is measured by the multiple correlation coefficient R^2 (all p-values below 0.0001, n = 5200). Only the predictions of the M_h linear model are represented, the full line shows the fit for Hortonian networks, the interrupted line shows the fit for non-Hortonian networks.
on local dynamics in dendritic networks, the cohesiveness of local groups of patches in any network could be measured thanks to the clustering coefficient (Newman 2003, see Fortuna et al. 2006 for an application in population dynamics). These measures are used to characterize any kind of networks, and usually do not focus on the particular case of dendritic networks: as for connectivity measures, it might be necessary to first analyze the properties of these descriptors linked to this particular kind of spatial structure.

Relation between network connectivity and population demogenetics

We found evidence that population demogenetics in our networks was significantly influenced by connectivity in a rather surprising way. Mainly, for high dispersal, metapopulation size was strongly and negatively influenced by connectivity while patch occupancy variance was increased by connectivity, and for low dispersal, local extinction and genetic isolation by distance were clearly promoted by connectivity. For mean and variance of allele number as well as for global $F_{ST}$, the directions depended on dispersal level. We also found that metapopulation persistence was slightly and negatively influenced by connectivity. While the existence of correlations between population demogenetics and connectivity could be suspected, based on previous knowledge of classic metapopulation models (Hanski 1999), the direction of the correlations was less intuitive.

The understanding of these counter-intuitive results in the context of our model cannot be achieved without first considering two notable facts: 1) in dendritic networks, mean connectivity is strongly and positively correlated with variance of connectivity, 2) Hortonian networks generally present a higher mean connectivity. The positive relationship between mean and variance of connectivity implies a non-random spatial distribution of connectivity: in Hortonian networks, local connectivity is relatively higher between patches located near the extremities and poor between patches in the interior of the network. As a consequence, these networks are structured in a few poorly interconnected groups of patches. On the opposite, non-Hortonian networks present a better balance between local and long distance connectivity. This contrast is well illustrated by the distribution of neighbors number, more skewed and variable in Hortonian networks.

Depending on dispersal, individuals and genes may circulate well within each group but not between groups, which may create long-distance isolation by distance and limit the rescue effect of migration in some parts of the network. The dynamics of extinction in the first set of simulations (declining populations) confirmed this explanation: root patches often go extinct early, hence isolating large portions of the network from each others. As initially stated in introduction, there can only be one path to reach different patches in the network: when a root patch goes extinct, the metapopulation is temporarily or definitively split in two, and each portion then undergoes a shorter persistence time, due to its reduced size. This effect is more sensitive in Hortonian networks: connectivity as measured by the number of neighbors is lower near the root compared to non-Hortonian networks, since Hortonian networks present less branching between non-consecutive order patches. In the second set of simulations (quasi-stationary state), for high dispersal values, no local extinction is observed, but the patch occupancy is more variable when connectivity is high, which is in fact the premise of local extinction and the observed situation for declining populations. For low values of dispersal, this mechanism is also at the origin of genetic isolation by distance: a group of densely connected patches will share a common genetic pool, and might be strongly isolated from another distant group if one or several root patches go extinct. In some extreme cases, the two groups may even shelter different alleles, leading to a pattern known as private alleles in population genetics (Hedrick 2000).

This first finding needs to be confirmed by examining bigger networks and improving the network generation process, while also analyzing in detail the spatial structure of metapopulations (existence of clusters in demography and genetics). If true, it would have direct consequences on mechanisms like divergence and adaptation of populations living in contrasted networks. Any network presenting a high mean connectivity would imply higher isolation and thus either favour local adaptation provided local migration is sufficient for genetic variance to exist within each group of patches. Under a certain reduction of gene flow, it could increase the probability for local groups of populations to be driven into a vortex of consanguinity and demographic stochasticity with the risk of local extinction (McCauley 1991). Such mechanism between networks connectivity and populations structures may be difficult to demonstrate in natural systems: estimating local connectivity in real dendritic networks could be challenging because it requires knowledge of favorable habitat distribution over the network and the definition of a minimum habitat unit. A Horton’s law based classification could help to overcome this problem.

Perspectives and conclusions

To explore the relationship between network structure variability and population demogenetics in this first approach, we restrained our analysis to a single population model. The strength and direction of results may depend on this initial choice. There are at least four possible source of variation of the present results that now deserve a thorough investigation. First, the dispersal function has undoubtedly a major importance: oriented dispersal, philopatry, out-of-the-network movements, long-range movements, each of these options will quantitatively and maybe qualitatively modify our results (Clobert et al. 2001). Second, we used only one life cycle, adequate for short life span species with average fecundity. These two parameters are also likely to influence genetic drift at the patch level. Third, we assumed spatial homogeneity in habitat (i.e. constant carrying capacity in space and time). Releasing this assumption will either dampen or aggravate the role of connectivity in the network, depending on the distribution of habitat size and quality (Harrison and Hastings 1996). Finally, we used basic initial conditions in our simulations. Simulating different initial conditions could also be of interest,
especially under the scope of invasion biology (Facon and David 2006).

In our understanding of the effect of spatial structure on population biology, the comparison with existing theory is required. But such comparison can be seriously misleading without first unifying some key concepts of spatial structure. For instance, the measure of local connectivity may appear as a potential candidate to scale the results of metapopulation and dendritic networks approaches, because as we showed, it is correlated to demogenetics. Unfortunately, this measure strongly differs between the two approaches: in dendritic networks, its variance seems to be constrained, which is not the case in metapopulation models. The direct consequence is that, depending on space and time scales, local connectivity in dendritic networks can produce the inverse effect than what is expected in classical metapopulations. Comparing populations in dendritic networks and metapopulations probably deserves a translation of the metapopulation model into a network framework, instead of considering patches distributed in a homogeneous matrix (Campbell Grant et al. 2007). In the case of dendritic networks, local connectivity, if defined by the neighborhood of other patches, is structurally never homogeneous. The upstream-downstream physical gradient of real riverine networks may also generate major oriented heterogeneities in resources (river continuum concept, Vannote et al. 1980), usually correlated with patch size. In addition to the non-independence of distances between pairs of patches, these characteristics demonstrate the specificity of dendritic networks, which represent a special case of spatial arrangement, and deserve a special attention from the ecological scientific community. Current developments in the analysis and exploration of networks structure bear hope that such a unified approach is possible (May 2006, Montoya et al. 2006), even if few theoretical works are yet dedicated to the specific problem of dendritic networks.

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