
Canopy architecture and multitrophic interactions

Introduction

Predator–prey, parasitoid–host, and other arthropod interactions do not occur in a vacuum, nor in a featureless world, but in a highly structured and complex environment. This basic observation has triggered numerous theoretical and empirical studies at the population level. Many are centered on the dynamics of populations occupying different patches (summarized in Hassell, 2000). A metapopulation framework implies a spatial arrangement of patches and movement of predators between them. However, once in a patch, a homogenous spatial situation is again assumed, and predators search at random. In fact, we know of very few examples of arthropod predator–prey or host–parasitoid studies which do incorporate the geometry of the environment at a smaller scale than a patch. In particular, we do not know any study that satisfactorily quantifies the architecture of the plant canopies and its influences on the outcomes of the interactions. This is surprising given that a great majority of predator–prey and parasitoid–host interactions occur in vegetation. Filling this gap is the thrust of this chapter.

The disregard for the architecture of the environment, in particular plant architecture, has two explanations. First, concepts and methods for mapping and modeling plant architecture have been developed only recently, i.e., mainly from the 1980s. Plant architecture, in particular tree architecture, has been the subject of intense research for quite some time (see for example Halle and Oldeman, 1970; Halle *et al.*, 1978), but this work was of a qualitative nature. Thus, the knowledge of how to measure and model plant architecture is too recent to have penetrated all fields of ecology. Plant canopies are highly complex modular structures that can be

described both in topological and geometrical terms. Topological information specifies the physical relationships between the different components of the structure while geometrical information specifies, *inter alia*, the shape, size, and spatial location of the components (Godin *et al.*, 1999). The architecture of a plant is an emergent property of its morphogenetic rules. Several ways to model morphogenetic rules have recently been proposed and the field is very active (see Room *et al.*, 1996; Michalewicz, 1999; Pearcy and Valladares, 1999; Gauthier *et al.*, 2000; Parker and Brown, 2000). Second, modeling interactions without paying attention to the fine-grained structure of the environment enables us to use variants of diffusion equations, for which a large body of knowledge is available (see Tilman and Kareiva, 1997; Shigesada and Kawasaki, 1997; Turchin, 1998). As comfortable as these assumptions may be, we are left with a large number of interactions for which a consideration of the geometry of the environment seems mandatory. The following example illustrates the kind of situations we envisage and the type of problems we would like to solve.

Imagine a ladybird beetle moving through vegetation, searching for prey of low abundance. Most of the stems and leaves and other structures the beetle explores are void of prey. Except for a few locations with hosts, and a few more with “hints” to the predator such as honeydew drops, the animal is moving in an empty “maze.” The “maze” constrains its movement by determining which routes are possible and which are not and is characterized by having components of both order and disorder. The animal itself makes different behavioral decisions in seemingly similar conditions, i.e., it also displays some degree of “randomness,” real or not, in its movement rules. Finally, the distribution of prey is most likely clumped, implying that the travel time between clusters of hosts will be very long. These long journeys will be spent finding a way through the maze.

The above description calls for a thorough understanding of at least three components of the multitrophic interaction: (1) the architecture of the environment, (2) the distribution of prey in the environment, and (3) the intrinsic movement rules of the predator. It is only after we have all three components that we can answer the following questions:

- What is the relative impact of plant architecture and prey distribution on predator searching efficiency?
- How is the risk of predation distributed among prey?
- Are the basic laws of diffusion equations valid, such as the linear increase mean square displacement?

- If yes, under which conditions can we disregard the architecture of the environment and use a “mean field” approximation?
- If no, what are the consequences of the anomalous diffusion in terms of individual and population parameters?
- Finally, how much biological realism must be sacrificed to construct a robust model for plant architecture and animal movement?

The above questions would be best answered by blending harmoniously the two themes of movement processes and geometrical systems. In practical terms, however, it is much easier to emphasize one of the themes and simplify the other. Thus, this chapter has been written from the perspective of a predator foraging for stationary prey in plant canopies of given architecture. Hence, we do not deal with modeling plant architecture *per se* and point the interested reader to the above entry points in the literature. The framework advocated here could easily be extended to nectar foraging and pollinator movement (see for example Pyke, 1978; Ganeshaiyah and Veena, 1988), but these are not multitrophic interactions as understood here. A treatment of these interactions along the lines described in this chapter has not been attempted so far. Also untouched is an aquatic perspective on these issues, as vegetation does act in a very similar way on predator–prey interactions in aquatic environments (see for example Russo, 1987).

The organization of the chapter is as follows. We first conduct a stock-taking of the published works on arthropod interactions in which plant architecture has been studied. While we consistently use predator–prey systems for simplicity, parasitoid–host interactions can be analyzed in the same way. We will see that some of the ideas can even be applied to phytophagous insects, as they must also solve the problem of resource location in a highly heterogeneous environment. Second, we explore the impact of plant architecture on the efficiency of the predator. Then, we turn to the population level and analyze the impact of plant architecture on predation rate. The dozen or so studies provide highly useful information on several aspects, but concomitantly give a somewhat fragmented perspective. The need for a synthesis is obvious, and we present a summary of ideas emerging from the study of random walk in a random medium. We advocate this framework as the best available to examine multitrophic interactions in plant canopies, as simply observing predators moving in plant canopies is not sufficient for tackling the above questions. We end the chapter by calling attention to several other fascinating and unexplored aspects of multitrophic interactions in complex environments.

Canopy geometry, prey distribution, and predator movement: a stocktaking

The aim of this section is to review the few publications demonstrating how the complex geometry of the plant leads to a heterogeneous distribution of prey and a heterogeneous distribution of predator effort. Andow and Prokrym (1990) suggested that there are three components of plant architecture relevant to foraging predators and parasitoids: (1) the plant size and surface area, (2) the structural heterogeneity among plant parts such as flower heads and stems, and (3) the connectivity of the plant parts. Their experiments approximated the structural complexity of plants by providing paper panels of different geometries to the egg parasitoid *Trichogramma nubilalis*. The number of parasitized egg masses of the host-moth *Ostrinia nubilalis* was analyzed as a function of the complexity of the paper panel. They made the important distinction between two different mechanisms acting on parasitism rates. On the one hand, a parasitoid may find the hosts more or less easily due to the structure of the environment, given the same searching intensity. On the other hand, parasitoids may forage with different intensities, irrespective of the presence of hosts, but as a function of the complexity of the environment. Structural complexity caused a threefold decrease in parasitism rate between the simple and complex environments. Part of the decrease in parasitism was due to the fact that *Trichogramma* searched simple surfaces devoid of hosts more intensively than complex ones. The major implication of this work is that decision rules such as giving-up time are influenced by the structural complexity of the environment *per se*. The results obtained by Andow and Prokrym (1990) were later corroborated by similar results by Lukianchuk and Smith (1997) using a different *Trichogramma* species and greater surface complexity. These important results have yet to be incorporated into works dealing with foraging in realistic complex environments.

Given the highly structured environment of plant canopies, prey will not be randomly or evenly distributed in the canopy. Nor do predators forage randomly or evenly. They tend to follow the structure of the canopy, but sometimes only partially. For example, the aphid parasitoid *Aphidius rhopalosiphi* spends most of its time on the leaves and little on the ear of wheat, the preferred feeding site of its aphid host *Sitobion avenae* (Gardner and Dixon, 1985). The parasitoids were reluctant to move on to the ear and normally spent little time there. Another parasitoid of

aphids, *Aphidius funebris*, attacks its host in a typical body posture that requires it to attack from leaves adjacent to the host colony (Weisser, 1995). A similar problem of prey accessibility was observed by Grevstad and Klepetka (1992), who found that aphids on *Brassica oleracea caulorapa* were mainly located on the middle of the underside of leaves, an area ladybird beetles could not get at because they could not grip to the undersurface. Consequently, the beetles tended to follow leaf edges and stems rather than the flat surface. Leaf edge is also the preferred route taken by the predator *Anthocoris confusus* during its search for its aphid prey (Evans, 1976). Predators moving in plant canopies composed of needle-like structures rather than leaves encounter similar problems. As described by Vohland (1996), needle density is higher in the upper and outer sectors of pine trees. This strongly influences the time spent by the older stages of the coccinellid *Scymnus nigrinus*, which spend most of their time there. This is also where prey densities are highest. The one-dimensional geometry of the needles "guides" the predator to its prey, and small larvae were very reluctant to cross over the shaft between bark and needle, where the prey feeds. Finally, using normal versus leafless peas, Kareiva and Sahakian (1990) demonstrated that the importance of plant morphological variation to herbivores sometimes becomes apparent only in a multitrophic framework. They demonstrated that different species of ladybirds were less effective in the normal peas, as they fell off the plants more often than in the leafless canopies. In contrast, whereas plant canopy architecture can impede predators by making the "maze" complex, it can also influence the aggregation of prey and predators, as nicely demonstrated by Kaiser (1983) using artificial arenas. He showed that borders influence both prey and predator spider mites in such a way that both stay more often along borders. The shorter the total length of borders, the higher the probability of contacts. As a consequence, different leaf forms of the same area can lead to different predation rates.

These examples show that the spatial coincidence of prey distributions and predator foraging effort is a key aspect of the interaction. They also demonstrate that descriptions of predator movement and prey distributions anchored in a framework based on homogeneous environment are not realistic. Obviously, it will often be difficult to quantify the effect of plant architecture on predators, because prey may change their behavior and location in the presence of predators, and vice versa.

Canopy geometry and predator movement: implications for multitrophic interactions

The effects of the complex geometry of plant canopies operate at both the individual and population levels. We first focus on the efficiency of predators, a behavioral trait, as function of plant architectural complexity.

The efficiency of a moving predator can be defined in many different ways that reflect the influence of plant architecture. Isenhour and Yeargan (1981) defined a measure of efficiency of explored regions as the distance traveled per encounter with a prey. They found very large differences for the bug *Orius insidiosus* attacking thrips on soybeans. The efficiency was at least an order of magnitude higher on the petiolus junction and on the midrib than on the leaf periphery. Efficiency can be also defined as the speed at which an animal travels a given distance. By varying the degree of bean-plant leaf overlap, Kareiva and Perry (1989) created two scenarios for the ladybird *Hippodamia convergens*: a highway and a gap situation. The highway situation enabled the ladybird to travel four times further (net displacement) per minute. The difference was mainly due to the high frequency of reversals in the gap situation. This fascinating study needs confirmation, as advocated by the authors themselves. This example is highly reminiscent of percolation theory, in which the probability of reaching a given point in space or the probability of crossing the whole medium is a function of the connectance between elements (Stauffer, 1985). Efficiency can be also defined as time allocation to given tasks. Suverkropp (1997) found that decreasing the time allocated to *Trichogramma* searching in a single plant increased the attack rate. While a longer search on a plant does of course increase the likelihood of finding an egg mass on that plant, the time spent is better allocated to checking other plants, given that hosts are randomly distributed among plants. This is an interesting way to avoid the complex architecture of canopies: instead of getting lost in complex structures, abandon them quickly and move somewhere else. Finally, efficiency can be synonymous with attack rate, which is the number of aphids killed per unit time. Grevstad and Klepetka (1992) found that the attack rate of four different ladybird beetles on aphids was much more influenced by the plant on which they foraged than by the ladybird species. This was due to differences in encounter rates, which were again function of plant species rather than

beetle-specific. The rate at which beetles fell off the plant was also a function of the plant species, in particular the slipperiness of the plant surface.

We now turn to the population level and analyze predation rates as function of plant architecture. The interplay between host density and plant architecture in determining parasitism rate at the population level has been worked out for an apple leaf miner by mapping both the architecture of trees over three years old as well as the position of unparasitized and hosts parasitized by *Cirrospilus vittatus* (Casas, 1991). The visit of a female parasitoid to a tree results in the parasitism of one or more hosts. While the first host is assumed to be chosen at random within the tree, further hosts can be parasitized, at random, within a spherical radius of 40 cm. The center of the moving sphere is the host currently under attack. In a young tree, parasitism resulting from a single visit made by a foraging female is usually restricted to hosts on the same branch, as most of the neighbor leaves within the sphere are on the same branch. Older trees have more branches and hence a more complex architecture. Attacks by a parasitoid then include different branches because they often intermix. In these cases, females no longer follow branches individually. As the number of hosts parasitized per attack is low due to the low fecundity of this species, one can expect inversely density-dependent parasitism per visit. In fact, parasitism rates at the branch level will be lower on older trees, as the attacks resulting from a single visit will be spread over several branches (Fig. 8.1). The relationship between the movement of the individual parasitoid (dimensions of the sphere of activity) and the tree architecture (dimensions and relative location of the branches) is of prime importance.

Using artificial plants of varying architecture, Geitzenauer and Bernays (1996) found that paper wasps attacked tobacco budworms at higher rates in architecturally less complex canopies. The mechanisms were behavioral, as it took them less time to locate hosts in the simpler canopies. The giving-up time was also higher in those plants. Also using artificial models, Frazer and McGregor (1994) showed major differences in giving-up time of a coccinellid beetle as a function of the form and angles of attachment of stem and leaf models. These differences are expected to result in major differences in the density of predators in a given crop and major differences in attack rates. All architectural characterizations of plant size, height, leaf number, leaf surface area, and branch number were negatively correlated with the attack rate of *Leptomastix dactylopii*, a parasitoid of the citrus mealybug (Cloyd and Sadof, 2000). The form of the func-

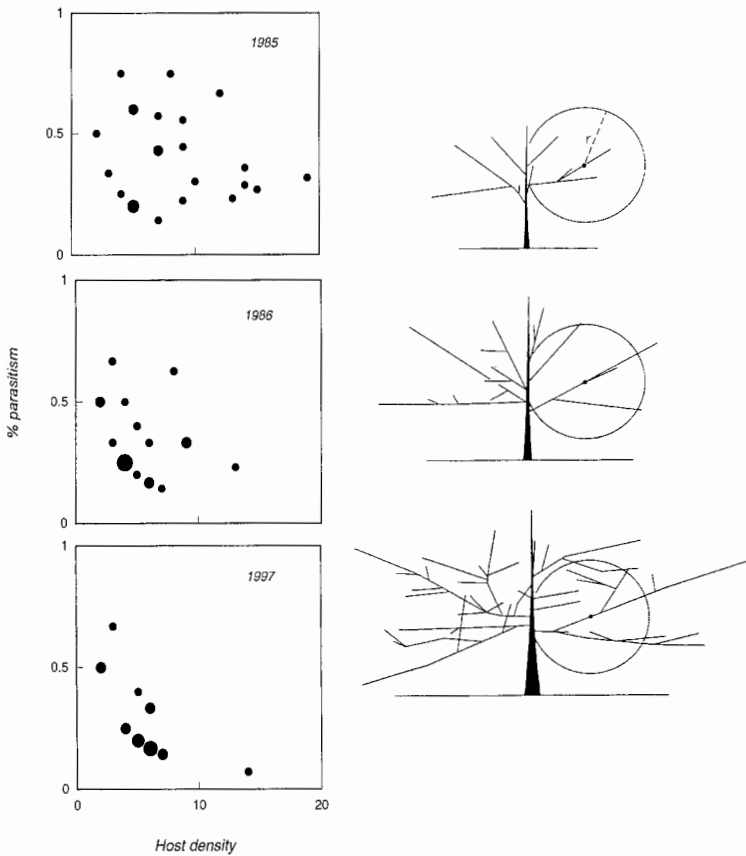


Fig. 8.1. Parasitism at the branch level per year in a tree (left) and canopy architecture of the tree during three successive years (right). Only branches bearing hosts are represented. The radius determining the volume in which a host can be attacked from a given location is also given.

tional response may also change as function of plant architecture. This may have a profound effect on the stability of predator–prey relationships. Messina and Hanks (1998) described a shift from a functional response type II to type III of a ladybird beetle foraging for aphids on two different plants. The shift was due to a density-dependent change in the proportion of aphids in refuges, such as rolled leaves, on one of the plants.

The general message from these studies is that plant architecture has major influences at different levels of multitrophic interactions: at the behavioral decisions of predators, on their own efficiencies, and on the

predation rate. It also influences the prey distribution and the spatial coincidence of prey and predators. We have seen one example where the influence of the first trophic level (plant species) on the third level (efficiency of predators) can be even bigger than the influence on the second trophic level (prey species). Unfortunately, these studies give a scattered view of the problem, but a general framework to deal quantitatively with the pervasive influence of the geometry of the environment is currently unavailable for ecologists and is sorely needed. We think that one based on random walks in random geometries could address most of the issues involved. This is our next topic.

Random geometry of the environment and particle movement

We momentarily leave ecology and enter a very active field of research in statistical physics. It covers two distinct themes: the movement of a walking particle and the geometry of the structure in which the particle is moving. We will deal with random movement of the random walk type, where the walker advances one step in unit time to a nearest neighbor site. For the geometry of the environment, we will assume lattice structures, either of a deterministic or random nature. Lattice structures are discrete versions of space that consist of sites connected to their nearest neighbor sites by bonds. We first describe well-known facts about regular diffusion in a regular lattice and continuum and then move on to more complex environments. We focus on random environments, as we think they better represent the architecture experienced by real insects. Movement in a tree-like structure, the comb, is used as an example to illustrate the effect of randomness in the environment's geometry and the effect of bias on the diffusion properties of the particle. We highlight the breakdown of many assumptions underlying the diffusion equation approximation.

Regular diffusion

Let us consider the most simple random walk in an homogeneous environment, the line $(\dots -4, -3, -2, -1, 0, +1, +2, +3, +4, \dots)$. The particle hops with steps of $+/-1$. The particle starts at 0 and moves towards the left with probability p and towards the right with probability q . For a small number of steps, it is possible to calculate the exact location of the particle after n steps using the binomial distribution. As an example,

assume $p = 0.6$, $q = 0.8$, and $s^2 = 4pq = 0.96$. After 40 steps, the probability of being no further than 10 steps from the origin is 0.68. After 1 million steps, the particle's position will lie almost certainly within a mere 4000 units of its starting-point. In other words, the particle does not move very far from the origin, even after many steps. Working out these probabilities becomes tedious when the number of steps becomes large, and we can make use of the central limit theorem and related theorems of probability theory to find continuum limits of random walks. By using limiting arguments, it is indeed possible to produce differential equations describing the continuum limit of this walk in both space and time. In other words, we give up the lattice structure and enter into a continuum, another homogeneous environment. For simplicity, we use a one-dimensional environment. The position of the particle $X(t)$ becomes then the Gaussian limiting distribution, N (at D^2t), which is the outcome of the diffusion equation, or Brownian motion with drift a and variance D^2 (Fig. 8.2).

Large deviations are rare occurrences in the Gaussian distribution. Indeed, a Gaussian variable with fluctuations σ diverges from the mean by more than 2σ in only 5% of cases. Fluctuations of more than 10σ are almost impossible, with a probability of 2×10^{-23} . The main advantage and the importance of the central limit theorem, which is the basis for the Gaussian limiting distribution, is that only very few quantities are retained from the observed dispersion process. Its detailed structure is lost in the tails that vanish with time. Among the statistics of interest that can be easily obtained are, for example, the diffusion coefficient D and the mean square displacement. It is a convenient means for measuring dispersion of the particle from the origin and increases linearly with time for diffusive processes (i.e., regular diffusion). The number of different sites visited, called the range, is also easily calculated.

We just showed above that discrete random walk processes can be used to generate continuous time processes by taking a continuum limit in both space and time. It is also possible to generate a continuous-time process on a lattice structure, i.e., keeping space discrete, by the use of linear rate equations (Weiss, 1994). Finally, one can also apply a very useful approach, the continuous-time random walk model. It has the advantage of having well-defined steps taking place at well-spaced times. Specifically, one can use a lattice structure and a particle moving between sites where it remains for a given sojourn time t , following some prescribed distribution (Weiss, 1994). Sojourn time is defined as the time

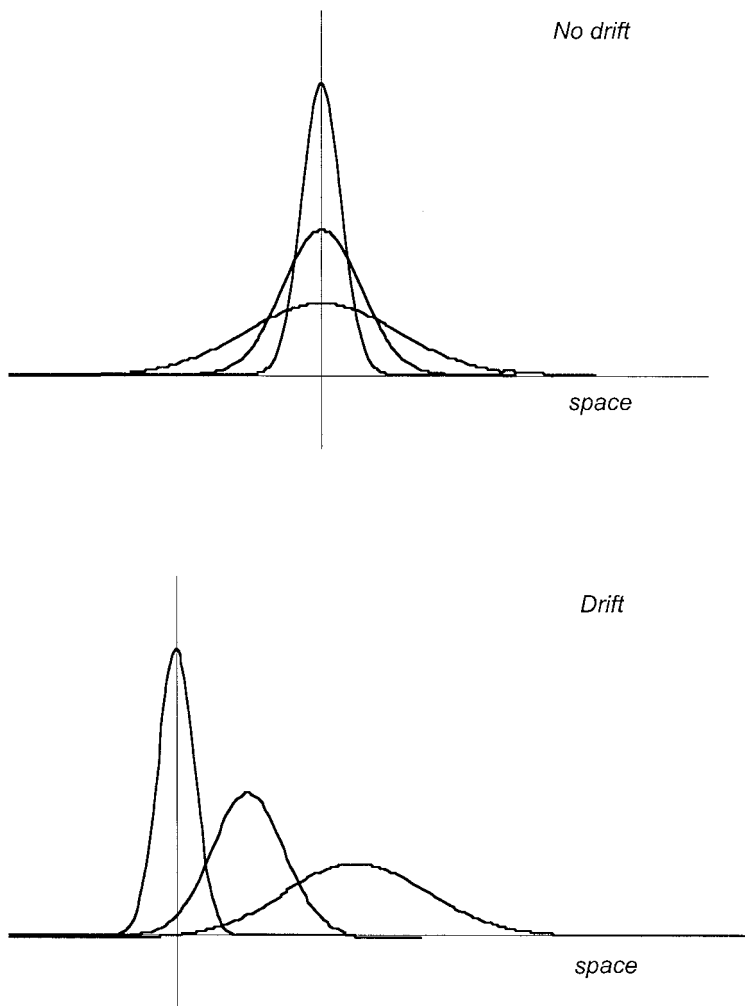


Fig. 8.2. Spread over time of a particle moving according to Brownian motion, without (top) and with (bottom) drift.

spent in one state before moving to another state. Random walks in a homogeneous environment in which the step-length distribution has a fat tail (i.e., long displacements occur relatively often) can change the basic rules of diffusion. In those distributions, the very long displacements do determine the overall dynamics of the system (probability of reaching a location, mean square displacement, etc.). The process

becomes superdiffusive, meaning that the particle moves quicker than in the normal diffusion process. This is shown by considering the mean square displacement that increases with the power of time t^γ , with $\gamma > 1$ (for so-called Lévy walks, see Drysdale and Robinson, 1998). These distributions have been found to be a valid approximation for several species of animals, including insects (Viswanathan *et al.*, 2000). In biological terms, such distributions imply that the likelihood of finding a predator far away from its starting location in a relatively short time is relatively high.

Random environments

Heterogeneity in the environment can be modeled in different ways. One way is to use deterministic models, such as those developed for fractals, percolation, etc. This will not be pursued here, but we refer to Halvin and Ben-Avraham (1987) for an in-depth treatment. Another approach, random environment modeling, is to consider one sample of the environment (a plant) as a single realization of an ensemble (a population of plants). The local properties of the realization, such as the location of gaps in the canopy, are determined following some stochastic process. The position of a particle, and all the statistics associated with it, depends on the history of the particle in the given environment and on the environment itself. Let us denote one realization of such an environment, a single plant, with ω . This environment will remain, for the sake of simplicity, constant through all the walks by the particle. One then has to distinguish two different ways of calculating averages: one over the environment ω and another one over the ensemble of possible environments Ω , the population of plants. This averaging gives the average behavior of the particle in an averaged environment, probably the description nearest to the heart of ecologists. It is only after the second averaging that one can appreciate the general features of the system. In practical terms, it requires the ecologist to map several canopies and predator paths and to come up with a probabilistic model describing both canopy geometry and predator movement.

The environment does not evolve with time in so-called quenched environments. By contrast, in annealed environments, a particle will never experience the same environment. For predators tracking prey in the vegetation, either model can be used, but we focus here on the simplest, the quenched environment. We will come back to annealed environments in the discussion. The randomness in the environment can have two kinds of effects on diffusion (Bouchaud and Georges, 1990):

- It may affect the value of the transport coefficients (velocity, diffusion coefficient, etc).
- It may affect the law of the diffusion process. For example, the mean square displacement may no longer increase linearly in time over long times. Anomalous diffusion, being super- or subdiffusive, corresponds to this kind of movement. In the superdiffusive case, the mean and mean squared displacement increase more quickly than linearly. The subdiffusive behavior leads to a sublinear function of time for both the mean and the mean square displacement.

In order to illustrate our ideas, we use below a specific model of a particle moving in a comb structure. But let us first contrast in general terms the propagation of two packets of predators, both released at the same end ($x=0$) of a one-dimensional space, and experiencing a drift in the same direction. Assume also that movement is made of hops, or steps of short distance. In the first case, the environment is homogeneous, leading to regular diffusion. In this case, the packet of predators moves as a whole, the location of the mode being the same as the location of the mean (Fig. 8.2). In the second case, the random geometry of the environment leads to long sojourn time at some locations, which then act as temporary traps. A large percentage of the predators experience usual displacement, similar to the predators experiencing regular diffusion. However, the longer the experiment, the greater the likelihood that all predators become trapped at some stage, i.e., hit a relatively rare but quite long sojourn time. In this subdiffusive case, the mode stays at $x=0$, and the mean position continues to increase, but at a decelerating rate (hence the name subdiffusive). This behavior is in contrast to the regular diffusion in which the mean progresses at a constant rate.

The random comb as an example

The comb structure bears strong similarities to real plant canopies as experienced by insects. It is a simple structure, made of a backbone and branches (Fig. 8.3). Framed in our topic, we ask for example how quickly insects move in a field given that they move up and down in the vegetation. Hence, one may envisage the vertical components of vegetation as acting as “traps” when considering movement in the horizontal plane. The problem is to characterize the movement along the backbone as function of the movement in the branches. Whenever a particle reaches a point on the x -axis it either makes a step along the x -axis with probability p or a step in the y -direction, along a branch, with probability $1-p$. The particle

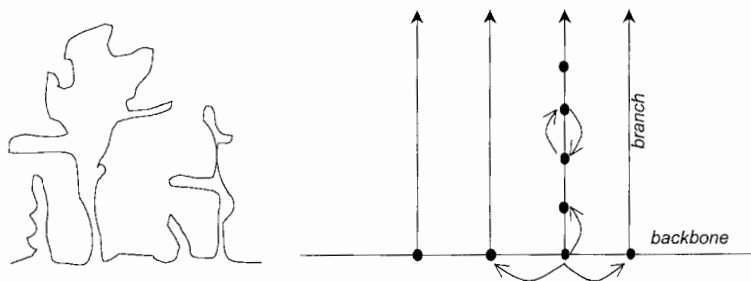


Fig. 8.3. The horizontal displacement of a predator moving up and down in vegetation (left) can be compared to a particle moving along a backbone and spending time in the vertical branches of a comb (right).

will then move within a branch following given jumping rates for the vertical movement. Once back on a point on the x -axis, the process repeats itself. The construction of this example is in three steps of increasing complexity:

1. We first assume no randomness in the branch length, which we set at infinity, and study the movement of the particle along the backbone. The observed movement cannot be modeled by the diffusion equation.
2. Then, we let the length of the branch vary and observe diffusive and subdiffusive behavior as function of the distribution used for modeling branch length.
3. Finally, using the branch distribution that would best correspond to real situations experienced by insects, we add vertical bias, i.e., the tendency for many insects to move up rather than down. A complete breakdown of the diffusive behavior is again observed.

We now demonstrate these three steps in detail.

Let first assume that there is no randomness in the structure and that the branch length is infinite. This biologically unrealistic assumption will be dropped later. The probability of return to the x -axis (τ_n) of a particle moving in one branch is the probability of return to the origin in a one-dimensional random walk for the first time at step n , $\tau_n \sim n^{-3/2}$. This probability distribution is somewhat special in the sense that its mean is infinite. The total time spent in branches is simply the sum of the N sojourn times spent in the different branches. As it is a sum of independent random variables, we can apply the central limit theorem and obtain the mean square displacement $\langle r^2(n) \rangle \sim n^{1/2}$, which is characteristic of anomalous diffusion. The anomalous transport is due to the average

infinite sojourn time of the particle in the branches. This leads to the occasional occurrence of very long waiting times. Let us recall that this breakdown of the diffusive behavior is obtained without any randomness or heterogeneity in the environment. However, this model is unrealistic due to the assumption of infinite length of the branches. The second step in our demonstration consists of adding randomness in the structure by assuming that the branch length (x) is given by the power law distribution $f(x) \sim \gamma x^{-(1+\gamma)}$. We obtain anomalous diffusion if $\gamma \leq 1$. If $\gamma > 1$, then the average branch length is finite and the diffusion is again regular at large times. A distribution with finite average branch length seems a priori the best analogy to situations encountered in nature by insects. The final “improvement” of our model is the addition of bias in the particle movement. Bias in random environments has two opposite effects (Halvin and Ben-Avraham, 1987). On the one hand, the particle is following the direction of the field, giving rise to a drift velocity. On the other hand, dead ends act as temporary traps from which particles escape by going against the flow. As a concrete example, let us consider the above case of regular diffusion on a comb by assuming that the branch length is given by an exponential distribution. Then assume that the bias is in the vertical direction. Thus, the particle has a higher probability of going upwards than downwards. Hence, one can ascribe to each branch a delay associated with the branch length. Long branches determine the overall behavior of the particle, as it is “pushed” towards their tip. One can show that the distribution of delays follows a power law distribution and that diffusion is again anomalous. This scenario corresponds in our multitrophic context to situations in which predators move preferentially upwards and may miss prey located on their way up.

Coda

The random geometrical structures in some dimension(s) of the environment cause delays in the movement of the particle in other dimensions. In the comb example, vertical movement in the branches delays progression along the backbone. The delay is generally characterized by a long tail of sojourn times that leads to anomalous transport along other dimension(s).

The study of processes characterized by time distributions with fat tails also brings to the forefront an important problem of scale. Some sojourn times are of the same order of magnitude as the total time of

observation. This leads to yet another breakdown of the regular diffusion approach, and its basis, the central limit theorem. In other words, there may not be enough time or steps in the process to attain an equilibrium distribution. By contrast, in the regular diffusion framework, the time-scale is defined by the mean value of the sojourn time distribution, while the physically relevant scale is defined by the variance of the step length distribution. There are no such scales in anomalous diffusion, as those moments diverge (Paul and Baschnagel, 1999).

These very general results, albeit borrowed from statistical physics, are bound to be true for predators moving in plant canopies. The implications are twofold. First, the geometry of the environment will determine the risk of predation of individual prey. Indeed, the probability that prey i located at X_i will be attacked by a predator j located at X_j within some time interval is obviously a function of their respective locations and the possible paths between them. The role and form of risk heterogeneity between prey in population dynamics is a major topic today as it determines the stability of the interaction (Gross and Ives, 1999; Olson *et al.*, 2000). Hence, the estimation of the probability distribution of risk among prey requires at some stage an estimate of accessibility of the prey in a given environment. Second, our understanding of spatial predator-prey population dynamics is built around the advection-diffusion framework championed in ecology by Kareiva and Odell (1987). They and others showed that the predicted spatial patterns, for example waves or uniform distributions, between prey and predators are the result of a delicate interplay between parameters describing random movement of the predator and its tendency to move towards prey (Wollkind *et al.*, 1991; Grünbaum, 1998, 1999; Cantrell and Cosner, 1999). Regular diffusion is often an unstated assumption of this approach. For example, one assumes that predators make many small steps in a relatively short time and that the distance covered is a small fraction of the available space. While these studies show how to incorporate microscopic details about the behavior and movement of predators into a macroscopic image of their distribution, they still lack proper model testing, as acknowledged by the authors themselves and others (Haefner, 1996). Hence, we do not know if these models are adequate, whether the spatial heterogeneity produced by the geometry of the environment is important, and how much a fuller treatment would increase our understanding of the mechanisms leading to spatial stability and our capacity to predict the spatial patterns.

Thus, we conclude that simple random walks in homogeneous environments and the regular diffusion approximation may be poor guides for understanding search strategies of predators and prey location in plant canopies. They are best replaced by a framework built around the concept of random walks in randomly or deterministically determined geometrically structured environments. Once such models are built and tested, simpler approximations can then be tested and the role of the fine-grained geometry of the environment determined.

Application of the framework

The only study we are aware of that follows the approach described above deals with movement of fruit flies foraging in apple trees (Casas and Aluja, 1997), a system similar to a multitrophic interaction as envisaged above. In our study, apple trees lacked fruits, and the framework provided the null hypothesis for inferring the influence of external stimuli, such as fruit color and odor, on the paths of foraging flies. We mapped three trees in cells, or sites, released preconditioned flies, and recorded their behavior and location. For modeling purposes, we discarded cubes devoid of vegetation and concentrated on cubes that could be used as landing points for the flies. This structure is an incomplete lattice structure, because anything within the cube is considered to lie on its lattice point and because empty cubes cannot serve as landing points. Since we were interested in the geometry of the path made by a foraging fly, we discarded both the time spent in the cube and any movement within the cubes. A move or step was defined as a change of cubes. Flies moved mainly to the nearest neighbor cells, but displacement within almost the entire range of possible values was observed. The model closest to the observations was a random walk with a position-dependent bias in the vertical component of movement. The movement rules, i.e., the probability of moving downward, upward, or horizontally, as well as the move distance, were estimated using foraging paths observed in one tree. The model was then applied to a second tree. Five models were built, spanning a range of simplifications in the rules determining the vertical component of movement.

We observed that flies, which generally enter the tree from the lowest half, move quickly upward into the bulk of vegetation. There are two complementary explanations for this behavior in terms of efficiency of movement. First, the presence of a bias not only increases the

speed at which flies move away from the starting location, but it also increases the number of sites visited, which is one way of describing the efficiency of a foraging path. As there is no point revisiting previously visited sites, a fly should avoid self-crossing, and the observed number of sites visited was indeed very near the maximum possible, indicating a high searching efficiency. Another interpretation for this behavior comes from the study of the diffusing properties of a set of random walkers (see Yuste and Acedo, 1999 and references therein). When the number of walkers starting at the same time from the same location is large, every possible site is visited in the neighborhood of the starting location within a very short time. But after a very long time, the walkers are so scattered that their paths hardly overlap, and the number of sites visited is simply the number of sites visited by one walker multiplied by the number of walkers. Such a mechanism is postulated as an explanation for the upward bias observed in the apple fruit fly. As flies tend to enter trees at the same height level, a bias in movement would thereby help a foraging fly avoid self-crossings and crossing areas already visited by other flies.

While quite sufficient in two trees, the model failed to reproduce observed movement patterns in a third tree. Testing models of movement in trees different from those in which they were developed is an acid test: models may fail because they are tree-specific. However, if they pass the test, we learn a lot about movement in plant canopies in general. The influence of canopy-to-canopy variation in geometry is best explained using the mean value of the range. The mean value of the range in tree A is dependent on the configuration of tree A (spatial arrangement of gaps in the canopy, geometry of branching, etc.). That mean value is found by observing or simulating many flies in tree A. However, our aim is to characterize movement in apple trees in general, and not just in tree A. Hence, our final interest lies in estimating the mean value over all apple trees, as explained in more general terms above. Thus, the failure of our model to predict movement in a third, geometrically rather different tree is the proof that our model was not robust enough. This is a strong case for developing a stochastic model for the plant canopy that produces an ensemble of canopies, out of which we could select specific realizations that would vary slightly from each other. In parallel, one needs to develop models of movement that are a genuine function of canopy geometry, rather than extract the rules from one environment and apply them as such to another environment.

Outlook

This chapter has been written from the perspective of a predator searching for immobile prey in a quenched environment. Strictly speaking, the description of our problem is valid only for a walking predator. Indeed, passing through connecting locations when moving from one location to another is unavoidable for a walking animal. A flying animal can however reach any point in a single step with some probability. The framework can easily be extended to flying insects once they are near or in a plant canopy. Many flying insects do not make long flights in this environment and follow the structure of the plant to some degree (Casas, 1990). Our approach can accommodate this behavior by using probabilities of moving from one location to another. This chapter has also paid scant attention to the third player in the game, the prey. Prey choose where they are going to end up on the plant, and their locations set the stage for predator movement. While we saw examples where prey are located in places which are difficult for predators to reach, we do not know of any study comparing predator movement foraging in plant canopies for naturally distributed prey versus artificially distributed prey. Coll *et al.* (1997) went a long way along these lines by distinguishing between the direct and indirect effects of plant architecture on predators. They found varying degrees of spatial overlap within plant canopies between prey and predators.

We end by touching on some effects of relaxing the assumption of quenched environments. First, we can allow the canopy architecture to change over time (annealed environments). Suverkropp (1997) calculated the dynamics of the probability of encounter of *Trichogramma* and egg masses of its host as a function of the growing maize canopy over a season. The leaf area was measured while the encounter probability was predicted using a data-rich model. While eggs of *Ostrinia nubilalis* are present, the plant changes from having three or four leaves to having fifteen. This represents an increase in the area to search of more than tenfold. The encounter probability, defined as the probability of a single female encountering an egg mass over a 24-h period, decreases from *c.* 0.3 to *c.* 0.05 during a season (Fig. 8.4). This observation suggests that most females will end the day without finding any hosts in the fully grown maize. This may be even true for their entire lifetime, given that they live for less than 12 days. At the time-scale of a fruiting season, prey may become highly susceptible to predation due to the fruit ontogeny, as

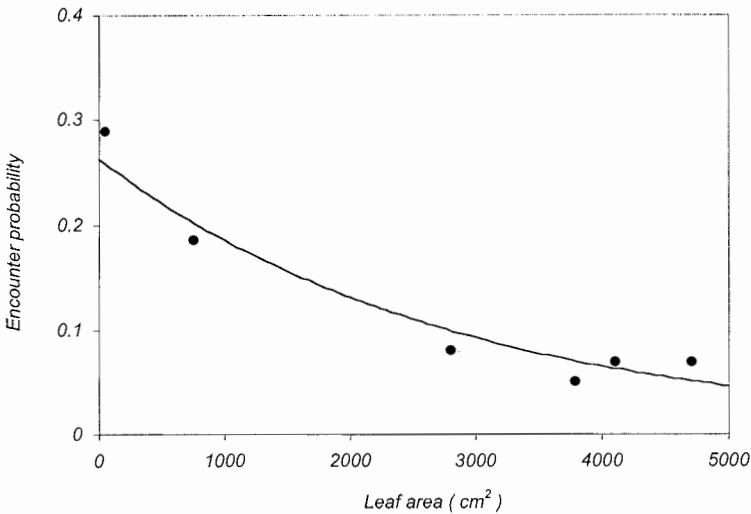


Fig. 8.4. Probability of finding a host by *Trichogramma* as function of the leaf area of maize growing over a season. (After Suverkropp, 1997.)

observed by Udayagiri and Welter (2000) for a mirid bug attacking strawberries. Fruit development resulted in a change in the fruits' structure and hence an increased accessibility of the eggs to its parasitoid. Changes in plant architecture over time-scales of years also influence interspecific interactions. C. R. Fonseca and W. W. Benson (unpublished data) describe ant succession and interspecific relationships during the ontogeny of Amazonian ant trees (tachigali). The canopy of a tree changes from an architecturally simple plant with a couple of leaves to a huge, highly complex canopy of thousands of leaves. More than half a dozen ant species colonize the plant and later disappear during this ontogenic succession. Such studies show that an increase in the complexity of canopy geometry fosters an equivalent increase in complexity of biotic interactions. Ontogeny of the insects suggests that the scale of an individual's range may also vary within its lifespan, as shown by Yang (2000) for a pentatomid predator.

A second possibility is to let the animal itself change the canopy's geometry. Many herbivorous insects are known to eat or tie leaves in very specific ways in order to avoid being eaten by predators (Djemai *et al.*, 2000 and references therein). Except for a few studies, modification of the canopy architecture to avoid predation and parasitism has hardly been

considered and rarely quantitatively measured. Overall, we believe that the most needed and lasting contributions along the lines described in this chapter will come from an integration of carefully designed field experiments encompassing detailed observations of prey and predator movements with modeling canopy architecture. To date, this is a virgin field of investigation.

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Multitrophic Level Interactions

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