Chapter 5
Disturbances and Coexistence of Species

Some conceptual models have been proposed to attempt an explanation of the mechanisms of coexistence of species inside environmental systems subjected to disturbances. Some of these models emphasize the role that disturbances (and, more specifically, their regime) may have in maintaining or altering the diversity of species observed in an area (Petraitis et al. 1989; McCabe and Gotelli 2000).

The Intermediate Disturbance Hypothesis (IDH)

According to this model, the effect that a particular disturbance event induces on the number of species in a community (and therefore on diversity) strictly depends on the frequency and/or intensity of the disturbance itself. Infrequent or low-intensity disturbances lead the community to evolve dynamically and to increase its structural complexity through a series of intrinsic processes, such as competition among species and a close adaptation to local conditions. In these communities, a dominance of the most competitive, specialized, and adapted species will be retained, at the expense of less-competitive species. At the opposite, in a community subjected to a high frequency and/or intensity of disturbance, those species with a higher ability to adapt to new conditions will be favored. In fact, in the process of recolonization, less competitive but more opportunistic species, adapted to variable and ephemeral environments, will benefit from the absence of competitors and will take advantage of the new space and resources. The new settlers will establish in the disturbed environments, thus becoming, at least in a first phase, the new dominants[1] in the community (Fig. 5.1).

[1]Many of these opportunistic species will be r-selected, differently from K-selected ones which are generally linked to more stable and less disturbed environments. In areas of intermediate disturbance, the IDH model thus predicts a coexistence of species with different strategies.

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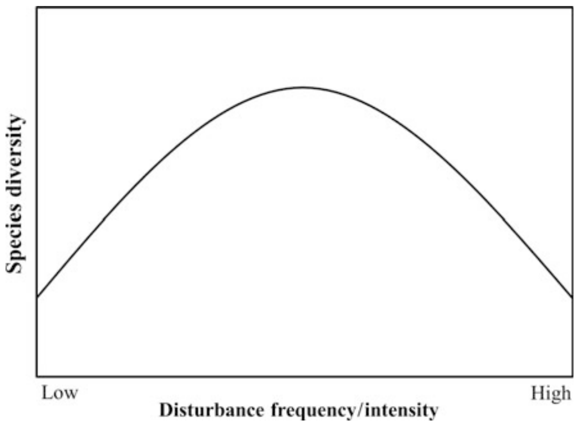

Fig. 5.1 The intermediate disturbance hypothesis which indicates that species diversity within a given patch should be highest at intermediate frequencies or intensities of disturbance (after Connell 1978) (from Hobbs and Huenneke 1992)

The species that were previously more competitive in a stable and low-disturbed environments lost their importance within the community. Due to their high specialization (stenoecìous species) and poor dispersive ability, they show lower predisposition to recolonize an area in the postdisturbance stage. In more extreme cases, where the frequency and/or intensity of disturbance are very high, a recolonization between successive disturbance events would not be possible, and the species forming the community will be reduced to those highly adapted to environments subjected to stress (McCabe and Gotelli 2000).

So, according to the IDH model, the presence of disturbances characterized by intermediate frequency and/or intensity can promote the coexistence and an increase of multiple species in the community (and therefore an increase of specific richness and diversity indexes). On the contrary, in response to events of low or high intensity and/or frequency, a more or less drastic decrease of biological diversity in the area affected by the disruption can occur. In the first case, specialists dominant in stable conditions will prevail, in the second the opportunists tied to unstable and ephemeral conditions will thrive.

There are many evidences pointing out that *intermediate* levels of disturbance (i.e., characterized by intermediate values of at least one of the attributes of the system, in particular, frequency and intensity) can lead to an increase in the number of species in the community (Connell 1978; Hobbs and Huenneke 1992).[2] According to the IDH model, conditions created as a result of an intermediate

[2]However, it is necessary to define the term *intermediate*. It can be considered with both an absolute and a relative meaning. For example, for a species with a relatively long life cycle a once a year recurrence of a disturbance may constitute an event of intermediate frequency (compared to a more frequent disturbance that occurs, for example, once a month or with a less frequent disturbance, such as once every ten years). Conversely, in a species that accomplishes its life cycle in a relatively short period (e.g., within a single year) the terms high, low, intermediate, will refer to completely different periods. In essence, the frequency of discrete events is closely related to and established on the longevity and life cycles of the species that suffer the disturbance.

disturbance event, will allow the coexistence of both strong competitors and specialists (k-selected species), and of opportunist colonizers (r-selected species). This will structure the community to comprise organisms differently characterized in terms of competitive ability, dispersive capacity, and disturbance tolerance (Crandall et al. 2003).

However, in the analysis of the effects of a disturbance, it is important to distinguish between intermediate mechanisms related to disturbance events that act internally to the environmental units (in which all organisms are simultaneously involved in the event: *within-patch mechanisms*), and mechanisms which do not act simultaneously in space and time, that is, with different regime in different patches of the landscape mosaic (defined as *patchy mechanisms* or also *between-patch mechanisms*; see Wilson 1994). In the latter case the species, although subjected to disturbances, may coexist in space or in time thanks to the presence of an environmental mosaic formed by *patches* at different degrees of disturbance and successional stage[3] (*successional mosaic hypothesis*). Within the mosaic, organisms will tend to move away from disturbed *patches*, dispersing and colonizing other *patches*, following the classic immigration-extinction (MacArthur and Wilson 1963) and the meta-population dynamics (Hanski 1994). According to Collins and Glenn (1997) the IDH model can be applied to both mechanisms (*within*- and *between-patch*; Wilson 1994).[4]

The IDH has been verified in various taxonomic groups and with different types of disturbance in marine, freshwater and terrestrial ecosystems. Particularly, high-productivity ecosystems have been studied (tropical forests, coral reefs; McCabe and Gotelli 2000). To date, however, this model has been applied mainly on sessile organisms. As they are unable to escape the environmental perturbations, they can be easily monitored in terms of number of individuals (density) and species (richness), as well as inside the temporal succession of plant communities, where diversity reaches the maximum values shortly after the beginning of the succession itself, to decrease afterwards[5] (Collins and Glenn 1997).

The IDH model is not, however, universally applicable. The evidence relating to a number of exceptions observed for at least some taxonomic groups and in certain

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[3]We mentioned the role of disturbance in promoting diversity at landscape scale, allowing the structuring of environmental mosaics (or eco-mosaics) formed by different *patches* due to the different intensities and frequencies of such events. This heterogeneity may play an important role in promoting the coexistence of species, especially in those landscapes where disturbances occur with intermediate frequencies and intensities (Roxburgh et al. 2004). In such contexts, the undisturbed *patches* may be used as a refuge by the susceptible species and act in the medium to long term as source areas of re-colonization (*source patches*).

[4]The distinction between the *within*- and *between-patch* mechanisms is also linked to the scale of analysis. If the total area in which a disturbance is acting (*disturbance area*) is wider than the sampling area, within-patch mechanisms are under study; if the disturbance area is less extensive than the sampling area, between-patch mechanisms are considered.

[5]In this case, the term *intermediate* is referred to the distance in time from the beginning of the post-disturbance succession.

conditions, have led in recent decades to a critical debate on the general and indiscriminate application of the model to environmental systems with characteristics different from those it has been tested until now (Crandall et al. 2003). One of the first criticisms showed that the IDH model proves to be too simplistic when compared with the complexity of the processes that give rise to the structure of the community (McCabe and Gotelli 2000; Roxburgh et al. 2004). Furthermore, the fact that, as mentioned earlier, the IDH has been clearly observed in only sessile organisms, does not allow to automatically conceive it as a model applicable to vagile organisms. Sessile organisms are in fact rooted to the substrate and, therefore, cannot circumvent the disturbance events. In this case, the colonization of non-disturbed areas is only possible via propagules dispersed by organisms.

The effects on vagile organisms may well be rather different. Being adapted to avoid possible disturbances, these organisms can get away from the sites where the event occurs and, in the case of frequent and/or high intensity disturbances, they can move away from the disturbed site, to return if conditions permit. This implies that in vagile species the expected decrease in species richness as a result of intense and/or high-frequency disturbance events cannot occur. Following extreme events, the large amount of sessile organisms that perish can also be a resource for mobile organisms and, contrary to the model prevision, an increase in the total number of individuals and species can be observed (Crandall et al. 2003). In conditions of maximum frequency and/or intensity of a perturbative event, the increase in density and richness in organisms at high vagility (such as many large vertebrates) may also initiate mechanisms of competition that are theoretically expected only in communities subjected to low-mid levels of intensity and frequency of disturbance (i.e., in stable or slightly disturbed systems). In that case, the big picture becomes more complex and unpredictable.

A further criticism has also shown how the IDH, assuming a high degree of interactions among species (e.g., competition), ignore the limiting role at the local scale of other physico-chemical factors that, together with the disturbance themselves, have their impact (Crandall et al. 2003).

Beyond the non-universality of the phenomenon and the criticisms that have emerged in recent times, the IDH is however a conceptual framework of reference that can explain the diversity present in biological communities according to the dynamics of extinction-immigration between patches. This model is configured as a complex pattern resulting from different mechanisms that help explain the coexistence of species in the medium to long term (Roxburgh et al. 2004).

The Huston Model of the Dynamic Equilibrium

According to this model, contrary to what the IDH model predicted, the species richness can reach a peak at a low, high or intermediate level of disturbance. Besides the entity of the disturbance, the species richness of the community may be affected also by additional internal features, such as competition and demography of populations of individual species. More specifically, coexistence and richness in the community may depend not only on the event of disturbance in itself, but also: (i) the rate of competitive exclusion internal to the community and (ii) the rate of growth of population.

This model offers a wider range of predictions than the classical IDH. It is based on the assumption that competitive exclusion can be directly correlated to the rate of population growth. As a consequence, the following predictions can be made.

- For low rates of both population growth and competitive exclusion, the highest species richness is achieved at minimum levels of frequency and intensity of disturbance;
- For intermediate growth rates and competitive exclusion, species richness in a community reaches a peak at intermediate levels of disturbance (as required by traditional IDH);
- For high rates of growth and competitive exclusion, species richness peaks at maximum frequencies of disturbance.

In essence, the difference between the IDH and the model of the Huston dynamic equilibrium is in the position of the maximum peak of diversity which, in the first case (IDH model), is achieved in conditions of intermediate frequency and intensity, while in the second (Huston equilibrium), depends on the rate of population growth (and, secondarily, on competition; Huston 1994; McCabe and Gotelli 2000).

The Model of Gradual Climate Change (GCC)

According to this model (Wilson 1994; Collins and Glenn 1997), the gradual change in environmental conditions (e.g., those due to the seasonality in temperate areas) prevents most of the species to achieve dominance in a stable community, thus enabling the coexistence of multiple species in different periods of the year.

The GCC and IDH models differ in many ways. In the first model, the environmental changes are gradual, in the second they are represented by discrete events and the effects are, in general, more pronounced. The two models can operate simultaneously in the community to explain the composition, structure and coexistence of species with different ecology. For example, at seasonal level, the GCC model can explain how gradual changes of environmental parameters may influence the phenology of species, allowing the coexistence over time of a higher number of taxa that will periodically change (turnover) on a relatively large territorial scale (e.g., regional areas). On a different scale (e.g., on individual sites), the IDH can instead explain the coexistence of species in the community as a result of disturbance events, the latter limited in time and space.

Although working at different scales, both mechanisms simultaneously affect biological communities. The impact of a local disturbance will depend, therefore, on how it will be placed along the time scale of manifestation of the GCC. For example, the same perturbation may cause different effects if it occurs in different seasonal periods. Because of the overlap of gradual (e.g., seasonal, GCC) and discrete (local disturbances, IDH) processes, tracing the mechanisms explaining the coexistence of species in a site can result in an arduous effort.

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