



REVIEW

Application of the intermediate disturbance hypothesis to flooding

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Abstract: We examine literature on flooding as a disturbance on both sessile and mobile organisms. The limitations and assumptions of the Intermediate Disturbance Hypothesis (IDH) are identified and examined. We conclude that research on plants supports the IDH. In contrast, mobile invertebrates and vertebrates rarely support the hypothesis. Therefore, we strongly encourage investigators to consider explanations beyond the IDH when explaining community dynamics following floods.

Abbreviation: IDH- Intermediate Disturbance Hypothesis.

Introduction

Disturbances are present in every natural system (e.g., Connell 1978, White 1979, Miller 1982). They can be broadly defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment” (Pickett and White 1985). Natural disturbances, such as wildfire, flooding, wind storms, and earthquakes, are typically examined in terms of major catastrophic events that originate in the physical environment. A disturbance can be an event as small as a pebble rolling over or as large as a tidal wave (White 1979, Sousa 1979a). At either extreme, microhabitats are created, which can be invaded by quick colonizers (Hemphill and Cooper 1983). This promotes the survival of individuals that are adapted to disturbances (Borner and Amoros 1996).

After a disturbance, initial colonization and immigration of new individuals result in a series of successional changes, which continue until the next disturbance (Lubchenco 1978, Sousa 1979a, Sousa 1979b). If an area lacks perturbation for an extended period of time, it will move toward a state of equilibrium where the most competitive species are dominant (White 1979, Miller 1982, Wootton

1998). Catastrophic disturbances usually have drastic effects, for example, decreased species richness and diversity, on communities, albeit recurrent disturbances increase environmental heterogeneity (Ward et al. 1999).

Research on disturbance in the past several decades has resulted in the development of the Intermediate Disturbance Hypothesis (IDH) (Connell 1978, Pickett and White 1985, Wootton 1998). This hypothesis states that high species diversity will occur at intermediate levels of disturbance (Connell 1978). The intermediate disturbance frequency that maintains diversity in a given community depends on the rate of competitive displacement in the system (Huston 1979). This frequency is typically the point at which the community is sustained as far from competitive equilibrium as possible (Huston 1979). In contrast, a community changes little when the disturbance interval is short relative to the time necessary for competition to exclude less competitive species (Miller 1982, De Leo and Ferrari 1993). Longer intervals will favor strong competitors, decrease species richness, and potentially create higher spatial heterogeneity (Connell 1978, Borner and Amoros 1996).

In this review, we examine flooding as a disturbance that affects both sessile and mobile organisms. Hydrological factors and magnitude of the disturbance cause floods

to vary (White 1979, Hemphill and Cooper 1983, Siebel and Blom 1998). The IDH has been widely applied to flood disturbances and the organisms found in these communities (Pickett and White 1985). We contend that the IDH generally pertains to sessile but not to mobile organisms with respect to flood disturbances. In particular, factors other than the degree of flooding must be considered when examining species diversity of mobile organisms. After introducing the IDH and discussing characteristics of flooding as a disturbance, we examine sessile organisms, mobile invertebrates, and mobile vertebrates in separate sections.

Intermediate Disturbance Hypothesis

The IDH has been widely applied to both various organisms and disturbance types (Pickett and White 1985). In plant communities, disturbances such as clearcutting, prescribed fire, and hurricanes increase herbaceous plant species diversity and abundance by increasing abiotic factors such as space, light, soil temperatures, and available moisture (Abrams and Dickmann 1983, Gillam et al. 1995, Zimmerman et al. 1996, Ross-Davis and Frego 2002). Repeated logging and short fire intervals in forests result in the decline of sensitive forest invertebrates that require both coarse woody debris and large deciduous trees. By contrast, natural and predictable disturbances such as fire increase habitat heterogeneity and invertebrate species diversity (Gurtz and Wallace 1984, Niemelä 1997, Bess et al. 2002).

Vertebrate diversity is positively correlated with herbaceous plant diversity (Isabirye-Basuta and Kasenene 1987, MacMahon et al. 1989, Imbeau et al. 1999). Small mammal colonization after disturbances, such as volcanic eruptions, fire, and clearcutting, depends on the availability of requisite food and shelter (MacMahon et al. 1989, Simon et al. 2002). Bird communities are negatively impacted by disturbances such as logging if the return interval is short because standing trees needed for nesting are decreased (Hutto 1995, Imbeau et al. 1999). Colonization by vertebrate species after a disturbance such as clearcutting and fire occurs only after reestablishment of the plant population, which provides food and shelter (Isabirye-Basuta and Kasenene 1987, MacMahon et al. 1989, Hutto 1995, Imbeau et al. 1999).

Research on sessile organisms strongly supports the IDH, because these individuals cannot escape perturbation, and in areas of intermediate disturbance regimes, sessile organisms often have high levels of diversity (Connell 1978, Pollock et al. 1998). The IDH has most often been supported by studies conducted in areas with high productivity, such as coral reefs and tropical forests. Stud-

ies on species with rapid growth rates, such as algae, also are more likely to support the IDH (Connell 1978, Huston 1994).

The IDH is often criticized for its assumptions and limitations. It assumes a strong degree of biotic interaction, while ignoring abiotic factors (Reice 1984). Disturbances influence species composition by altering ecosystem processes (Abrams and Dickmann 1983). For example, it does not consider how fire increases nutrient cycling, which favors specialists such as legumes (Abrams and Dickmann 1983, Masters et al. 1993). Another criticism is that it assumes interactions on a single trophic level and views organisms on other trophic levels as inconsequential (Wootton 1998). Disturbances may temporarily relieve the affected trophic level from competition, and cause intensified competition elsewhere in the food web (Barnes and Minshall 1983). For example, a disturbance at a lower trophic level would result in less competition at that level and subsequent prey shortages at higher trophic levels (Barnes and Minshall 1983, Reice 1984). Finally, it is impractical to apply the IDH to both sessile and mobile organisms. Mobile organisms are more likely to flee or seek refuge during a disturbance and often return to the area. These populations generally do not suffer substantial losses because of mortality after a disturbance. As a result, competitive exclusion may be more significant in determining the species present (Huston 1979).

Flooding

Hydrological factors cause the impact of flooding on the dynamics of aquatic communities to vary. Streams, rivers, and lakes are a few of the many types of aquatic ecosystems (Morisawa 1968). The hydrology of a stream or river is markedly different from that of a lake. Streams and rivers are open systems characterized by annual floods, as well as catastrophic floods, which cause pulsed periods of detrital input and temperature change (Barnes and Minshall 1983). Lakes, in contrast, are subjected to flooding and yearly turnovers as well as detritus input. Also, flow velocity is more constant in lakes than in streams and rivers because runoff and stream flow depend on rainfall and evapotranspiration (Morisawa 1968). The hydrologic characteristics of aquatic systems depend on geologic conditions such as topography of the watershed, rock type, and soil mantle. During a flood, these characteristics impact flow and deposition of sediments (Morisawa 1985).

Flooding is a disturbance that impacts both sessile and mobile organisms. Floods disturb landscapes by physically removing organisms, seeds, and other biomass that

may be in the perturbed area (Huston 1994, Howell and Benson 2000). Four factors contribute to the ecological effects of flooding: duration, flow velocity, season of occurrence, and frequency or the amount of time between floods (White 1979, Hemphill and Cooper 1983, Siebel and Blom 1998). These characteristics of a flood contribute to the degree of mortality or loss of biomass, growth and recovery of disturbed populations, rate of immigration into the disturbed area, and rate of competitive displacement (Huston 1994). Flooding duration impacts different organisms to varying degrees; a short-lived flood will flatten herbaceous vegetation with little mortality and cause temporary relocation of some mobile organisms (Stickel 1948). A long-lived flood will produce high plant mortality and delay return to the pre-flood community composition (Ferreira and Stohlgren 1999). Differences in flow velocity and geomorphical features cause patchiness of floodplain communities (Connell 1978, White 1979, Bornette and Amoros 1996, Ward et al. 1999). Season of flooding has a direct effect on vegetation (White 1979). For example, tree species that germinate later in the spring will likely avoid spring floods the first year, thus increasing the likelihood of surviving floods in subsequent years (Siebel and Blom 1998). In riparian zones, an intermediate flooding frequency maintains a stage of secondary succession, whereas longer flood intervals favor competitive exclusion, and shorter flood intervals favor early colonizers (Miller 1982, Petraitis et al. 1989, De Leo and Ferrari 1993, Bornette and Amoros 1996).

Sessile organisms

The IDH is supported by research concerning the impact of flooding on sessile organisms (Biggs 1995, Bornette and Amoros 1996, Pollock et al. 1998, Wootton 1998, Ferreira 1999). Most plants are rooted in the substrate and therefore cannot flee or seek refuge from rising floodwater. This inability to move, forces plants and other sessile organisms to contend with and adapt to disturbances. During a flood, plants can be flattened, lose branches, or be up-rooted by floodwater (Stickel 1948). However, floodwater can also aid in seed dispersal, provide moist nutrient rich sites for germination, and help maintain overall water levels (Howell and Benson 2000). The following paragraphs examine four studies of plants in which data support the IDH.

Studies of vegetation of meadows and woodlands in a frequently flooded wetland community on a coastal inlet of Alaska provide both observational and numerical data that support the IDH (Pollock et al. 1998). Researchers found that species richness and diversity increased as flood frequency increased. However, at extremely high

frequencies of flooding richness and diversity decreased. Intermediate flood frequency increases species richness and species diversity. The authors also noted that frequently flooded sites had little vegetation or were dominated by one or two plant species, usually quick growing taxa such as willowherb (*Epilobium* sp.) and bentgrass (*Agrostis* spp.), demonstrating the early stages of succession caused by disturbance. In addition, they state that five of the six sites displaying the greatest species diversity were at intermediate levels of flood frequency, further supporting the IDH.

In a study of vegetation dynamics of riverine wetlands in France, Bornette and Amoros (1996) found that areas exposed to frequent floods or to high intensity floods had low species richness and diversity. Therefore, higher levels of species richness and diversity were found when flooding created an intermediate level of disturbance, supporting the IDH. Infrequently flooded sites had species compositions very different from frequently flooded sites. One reason for this is that sediment creates a patchy landscape. Areas with high species richness have a greater diversity of soil types than areas with low species richness. This mosaic of soils is a result of flooding, and the deposition of sediments based on microtopography. It creates many different habitats in a small area, which allows colonization by different plants. They conclude that "floods resulted in the stability of the ecosystem through community composition, species richness, and diversity" (Bornette and Amoros 1996).

Species richness of mature trees in three distinct habitats within a floodplain forest of Central Amazonia, a lake, a stream, and a river margin, indicate a negative correlation between increased level of floodwater and species richness (Ferreira 1997, Ferreira and Stohlgren 1999, Ferreira 2000). They also show a negative correlation between length of flood and species richness. The lake area was inundated by floodwater for nearly 260 days a year, a long period, and had the lowest species richness of the three sites. The river and stream sites both exhibited flooding with an intermediate duration, leading to increased species richness, thus supporting the IDH.

Periphyton, mat-forming algae that grow on rocks in stream catchments, show increased species richness with increased flood frequency and flow velocity in New Zealand (Biggs 1995). However, extremely swift flow velocities remove large pieces of periphyton mats, decreasing diversity. Likewise, infrequent flooding leads to slow stream flow velocity, which favors filamentous algal species, again decreasing overall diversity. These findings support the IDH; intermediate levels of flooding increased the species diversity of sessile organisms.

These studies, along with many others, demonstrate that sessile organisms such as plants support the Intermediate Disturbance Hypothesis. Intermediate levels of flooding increase plant diversity, while extreme levels of flooding decrease plant diversity.

Mobile invertebrates

Aquatic invertebrates are abundant in riverine communities making them a crucial component of the ecosystem (Junk et al. 1989, Malmqvist 2002, Cardinale and Palmer 2002). They affect the cycling of nutrients and carbon by acting as an intermediate link between primary producers, primary consumers, and predators at higher trophic levels (Thorp and Bergy 1981, Barnes and Minshall 1983, Malmqvist 2002). Aquatic invertebrates have varying degrees of mobility, so they are variously affected following a flood; some move to protected regions, whereas others are swept to new areas (Lake 1990, Townsend et al. 1997, Robinson et al. 2002). Huston (1994) and Wootton (1998) proposed that research on mobile invertebrates and disturbance rarely supports the IDH. In the following paragraphs, we cite specific studies illustrating the response of such aquatic organisms to flooding.

Analyzing zooplankton data collected in the Po River, De Leo and Ferrari (1993) observed that, during floods, the species richness and Shannon diversity of zooplankton rise sharply. Their data support the IDH; i.e., if the disturbance is too frequent, there is no opportunity for most species to recruit successfully. Therefore, the highest species diversity of zooplankton is found at an intermediate degree of flooding. Similar results were observed by Townsend et al. (1997); both highly mobile and relatively sedentary invertebrates had a higher diversity at intermediate degrees of flooding.

Reice (1984) examined flood frequency in a macrobenthic stream community and determined that repeated flooding keeps fauna at depressed levels relative to undisturbed substrates. Also, after a disturbance, the community returned to its pre-disturbance state unless there were subsequent perturbations, which delayed the recovery. This study refutes the IDH, and simply shows that flooding alters the habitat of lotic macroinvertebrates and drastically reduces the total community size without significantly affecting the diversity. These results are similar to those of Death and Winterbourn (1995), who concluded that increasing disturbance frequency in streams reduces the time available for recolonization of benthic invertebrates before the following disturbance. Thus, increasing flooding frequency will lower species richness and diversity. This statement also is supported by Uetz et

al. (1979) who reported a lower diversity of arthropods in areas with more frequent floods.

Review of other studies (Gallepp 1977, Siegfried and Knight 1977, McAuliffe 1984, Lake 1990, Palmer et al. 1992, Wootton et al. 1996) reveals a variety of conclusions when applying the IDH to mobile invertebrates. Some investigators do not consider the assumptions and limitations of the hypothesis. These include interactions among and between trophic levels, abiotic factors, season of flooding, and life histories. Huston (1994) and Wootton (1998) proposed that the IDH is not widely applicable to all mobile invertebrates and additional variables and interactions must be considered.

Wootton et al. (1996) argued that the IDH is too simple and should be expanded to incorporate interactions among trophic levels. They manipulated the abundance of a predator-resistant grazer (caddisfly) in mesocosms placed in the South Fork Eel River in California and concluded that removing regular floods would cause an increase in predator resistant grazers which would, in turn, divert energy away from the food chain leading to predatory fish. Also, their survey of the biota of irregularly flooded rivers revealed a higher occurrence of predator-resistant grazers, and lower occurrence of both predators, and predator-susceptible grazers, as compared to rivers with predictable flooding. In general, examination of only a single trophic level would result in an incomplete conclusion.

Interspecific competition also plays a role in invertebrate population dynamics, because, flooding causes differences in a river's flow velocity (Siegfried and Knight 1977). McAuliffe's (1984) examination of flooding and interspecific competition supported the IDH. He found that flooding will displace some benthic communities of stream invertebrates and increase competition for space in suitable microhabitats. Thus, regular flooding resulted in competition limiting the distribution and abundance of individuals. This concept was further supported by Hemphill and Cooper (1983) who reported that flooding promotes the coexistence of two or more species by preventing a climax state.

The effect of flow velocity on caddisflies (*Brachycentrus americanus* and *B. occidentalis*) was studied by Gallepp (1977). He concluded that caddisfly populations did not change significantly when flow velocity was manipulated. Instead, the caddisflies were directly affected by abiotic variables, such as temperature and food availability. Lake et al. (1989) mimicked variations in flow velocity by raking riffle substratum. They also observed that this type of disturbance did not significantly alter the di-

versity of macroinvertebrate communities, although the diversity did increase briefly immediately after the disturbance.

Some aquatic invertebrates have adapted to frequent flooding that is temporally consistent. For example, the growth of some arthropod populations is delayed when flooding occurs in the spring (Uetz et al. 1979). Groups of organisms that are adapted to frequent flooding may dominate the area and reduce the diversity during the spring. Then, as the habitat becomes more suitable to other species during the summer, the diversity will increase and "peak" (Junk et al. 1989). Thus, annual cycles of diversity are often displayed by mobile invertebrates, making application of the IDH to these organisms impractical.

Invertebrates have different modes of dispersal and recolonization, which should be considered when applying the IDH to flooding (Palmer et al. 1992). Some species are mobile by adult flight and oviposition of eggs, and others can only drift or crawl (Lake 1990). Therefore, some aquatic invertebrates with a greater degree of mobility can escape floods or seek refuge in streambed interstices, whereas others can remain dormant in the water (Robinson et al. 2002). In contrast, individuals that float may be transported by currents to undesirable habitats during flooding (Siegfried and Knight 1977, Palmer et al. 1992). Lotic invertebrates typically recover quickly after a flood, attributable to refuge-seeking behaviors (Palmer et al. 1992), or flexible life histories (Scrimgeour and Winterbourn 1989).

These studies illustrate the assumptions and limitations of the IDH. Thus, interactions among and between trophic levels, abiotic variables, season of flooding, and type of mobility should be examined before applying the IDH to mobile invertebrates (Uetz et al. 1979, Fisher et al. 1982, McAuliffe 1984, Wootton 1998). Because these organisms play an essential role in the food web of aquatic ecosystems, they should be examined morphologically and in conjunction with other organisms and environmental characteristics. It is difficult to apply the IDH to mobile invertebrates, because there is a strong link between productivity and stability in aquatic habitats. In addition, there is a lack of information on the result of increased productivity on competition in stream communities (Death and Winterbourn 1995). Clearly, more research is needed to resolve the ways in which disturbances influence mobile invertebrates.

Mobile vertebrates

Sessile organisms must endure flooding and suffer from injury or mortality, whereas mobile vertebrates gen-

erally move to a refuge and avoid harm. However, destructive flooding may result in high mortality in fish, amphibian, and mammal communities (Blair 1939, Yeager and Anderson 1944, McCarley 1959, Turner 1966, Harrell 1978, Real et al. 1993). In areas of short-lived flooding, animals are typically able to evade the negative effects of flooding, causing increased survival rates. Fish are not swept downstream because they seek refuge and become less active during flood events (Ross and Baker 1983). Several mammal species avoid floods by taking refuge in nearby trees and shrubs (Anderson and Shapiro 1957, Wolff and Hurlbutt 1982, Kaufman et al. 1985, Ellis et al. 1997). Many mammals can also swim, which enables them to avoid drowning (Stickel 1948, Ruffer 1961). In the following paragraphs, we illustrate that flooding does not have the same effects on assemblages of mobile and sessile organisms.

Because flooding affects mobile vertebrates to a lesser degree than immobile organisms, vertebrate species diversity may not be a result of this disturbance because few individuals perish, and when flood water subsides, animals can return to their pre-flood home ranges (Hoslett 1961, Ruffer 1961, Blem and Blem 1975, Anderson et al. 2000). In addition, species diversity may remain relatively constant because, if animals are lost, immigration from surrounding communities will reestablish the original species composition (Fuentes and Jaksic 1988). As a result, few studies on mobile vertebrates support the IDH. Flooding as a disturbance does not usually facilitate high species diversity in these communities (Fuentes and Jaksic 1988, Mackey and Currie 2001).

In some instances, disturbances caused by flooding may support the IDH. Seegrist and Gard (1972) demonstrated this by examining rainbow trout (*Salmo gairdneri*) and brook trout (*Salvelinus fontinalis*) populations in a river with spring and winter flooding. Brook trout lay spawn in winter and fry hatch in the spring, making their eggs susceptible to mortality during winter floods. Conversely, rainbow trout spawn in the spring, but their eggs are still susceptible to spring floods and many perish. The two fish species compete strongly with one another for limiting resources, but their reproductive cycles, in conjunction with flooding, allow coexistence by controlling population numbers and preventing competitive exclusion (Seegrist and Gard 1972). Meffe (1984) studied interactions between a native fish species, the Sonoran topminnow (*Poeciliopsis occidentalis*), which is adapted to flash flooding, and an introduced species, the mosquitofish (*Gambusia affinis*), which is not adapted to flash flooding. Long-term coexistence between the two species

is facilitated by high mortality of the more competitive mosquitofish during flash floods.

Furthermore, most amphibians are especially vulnerable to flooding, specifically during their larval stages and immediately after metamorphosis (Bell and Lawton 1975). Amphibian diversity was found to be maintained by an intermediate flooding regime in a Mediterranean watershed by Real et al. (1993).

Flooding may also increase the diversity of mobile vertebrates in affected areas by providing and renewing resources. Flooding increases the variety and abundance of food, which benefits many fish species (Ross and Baker 1983). Additional nutrient availability may decrease interspecific and intraspecific competition and increase population numbers of those species using the resources. Flooding also causes an increase in avian diversity, because more nesting sites are available and food diversity and abundance increase (Shimada et al. 2000, Robinson et al. 2002).

Application of the IDH is limited because it generally does not apply to mobile vertebrates. These animals have the ability to avoid and survive disturbance. Without the removal of individuals from a community, competition may be high and, as a result, competitive exclusion may occur. In addition, the diversity that exists among terrestrial vertebrates may be a result of diverse landscapes with several microhabitats and resources that can be differentially exploited by animal species (Fuentes and Jaksic 1988).

Discussion

The Intermediate Disturbance Hypothesis was proposed to explain high diversity in systems with intermediate levels of disturbance (Connell 1978). Unfortunately, this simplistic hypothesis is overused and, in many cases, accepted as the only explanation for species diversity in disturbed areas (Resh et al. 1988, Huston 1994, Wootton 1998). For instance, disturbance may increase habitat heterogeneity and alter food webs. Thus, increased species diversity in areas of intermediate disturbance would be a simple byproduct of resource variability or trophic interactions.

Research on communities of sessile organisms generally supports the IDH. Plant communities routinely show an increase in species richness in response to intermediate levels of flooding, and a decrease in species richness in response to extreme levels of flooding. The IDH is applicable because primary producers must endure disturbances, therefore directly affecting their diversity.

The IDH should not be widely applied to mobile organisms in aquatic systems. Specifically, research on mobile aquatic invertebrates rarely supports the hypothesis because of the organisms' ability to avoid disturbance and their varied life histories (Palmer et al. 1992, Robinson et al. 2002). In some cases, investigators have accepted the IDH without alluding to abiotic variables that were altered during flooding (Gallepp 1977). Thus, even in these cases, it is unlikely that data from further investigations would still support the hypothesis.

Most research on vertebrate communities does not support the IDH, because mobile organisms can escape disturbances (Anderson et al. 2000). In cases of high mortality, they can restore populations quickly with immigrants from surrounding areas (Fuentes and Jaksic 1988). Flooding can benefit species by reducing interspecific and intraspecific competition. Research on fish communities sometimes suggests that these vertebrates may follow the IDH, because flooding allows for species coexistence (Seegrist and Gard 1972, Meffe 1984). Species composition in most animal communities however, is maintained by competitive exclusion, and diversity is often a result of habitat and resource heterogeneity (Fuentes and Jaksic 1988).

We do not refute the IDH in all cases, but simply state that further investigation is needed when examining disturbances. Floods vary in many factors, so it is difficult to examine only one aspect. Thus, we suggest that multiple effects of disturbance be examined simultaneously. Factors such as flood predictability, light attenuation, substrate composition, moisture availability, and flow regime should be considered, especially when examining sessile organisms and mobile invertebrates. In fact, these factors could be used to create a more general disturbance hypothesis. Our review of literature on disturbance has revealed a void in research involving the marking and recapturing of individual organisms. Observation of riparian vertebrate communities before and after flooding and quantification of mortality and extirpation of marked species present after flooding events would indicate their response to disturbance. Researchers should consider mobility during different life stages and abiotic consequences of disturbance, as well as inter- and intra-specific competition when applying the IDH to complex, natural systems.

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