Review article

Reevaluating the Theory of Gap Dynamics Using Studies of Typhoon Disturbance at the Fushan Experimental Forest, Northeastern Taiwan

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【Summary】

The theory of gap dynamics generalizes disturbance-diversity-forest dynamics relationships but is hotly debated. Studies of interactions between tropical cyclones and forest dynamics at the Fushan Long-term Ecological Research Site in northeastern Taiwan, where typhoon disturbances occur on an annual basis, indicate that gaps created by disturbances do not always differ from the non-gap understory in important physical conditions such as light availability and variability. Therefore, shade-tolerant and -intolerant species can coexist in both gaps and the non-gap understory. In such forests, gaps are not indispensable for the establishment and growth of shade-intolerant species as postulated by the theory of gap dynamics. Thus, it is important to focus on specific environmental conditions rather than the gap versus non-gap status when discussing gap-biodiversity-forest dynamics relationships. In the era of climate change characterized by more-frequent climate extremes and natural disturbances, we should move beyond generalizations and directly address the processes leading to the observed relationships among disturbance, diversity, and forest dynamics.

Key words: theory of gap dynamics, disturbance-diversity-forest dynamics, typhoon disturbance, climate change, Fushan Long-term Ecological Research.

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學術論述

以台灣東北部福山試驗林颱風研究
重新評估孔隙動態理論

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摘　要

孔隙動態理論為擾動、生物多樣性與森林動態之間的關係提出通則性的論述，但引起了廣泛的爭論。在每年均有颱風擾動的台灣東北部福山長期生態研究站，對熱帶氣旋和森林動態關係的研究指出，擾動造成的林間孔隙與非孔隙在重要的物理條件，如林下光照量與其變異程度，未必有顯著差異。因此，耐陰和不耐陰的物種可以共存於孔隙和非孔隙的林下。在這類森林中，不耐陰樹種並非如孔隙動態理論所假定的一定得依靠孔隙才能在林內存活和生長。在討論孔隙、生物多樣性、和森林動態的關係時，焦點應集中在環境條件的差異而不是孔隙與非孔隙的區分。在氣候變遷使得極端氣候和自然擾動更為頻繁的年代，更應該超越一般通則，直接探討導致吾人所觀察到的擾動、生物多樣性和森林動態之間關係的過程。

關鍵詞：孔隙動態理論、擾動多樣性與森林動態、颱風擾動、氣候變遷、福山長期生態研究。

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INTRODUCTION

Disturbances play an important role in characterizing ecosystem structure, function, and dynamics. The spatial scale of disturbance effects on biodiversity ranges from canopy gaps caused by a tree fall to the entire globe caused by an asteroid impact. Large disturbances can reset community development and initiate secondary succession, while in the absence of disturbances, a community will eventually reach a state in which shade-tolerant species dominate the late successional community (Whittaker 1953, 1974, Horn 1974). A key discussion in disturbance ecology is relationships among disturbance, biodiversity, and ecosystem dynamics. Disturbances have the potential to directly alter biodiversity through differential species removal and indirectly through modifying the biotic and abiotic environments and thereby altering competition among species (Glitzenstein et al. 1986, Hughes et al. 2007). Many theories, models, and hypotheses such as the intermediate disturbance hypothesis (Connell 1978), the dynamic equilibrium model (Huston 1979), and the theory of gap dynamics (Watt 1947, Shugart 1984), have been developed to describe and predict relationships among disturbance, biodiversity, and ecosystem dynamics. Among them, the theory of gap dynamics (Watt 1947, Shugart 1984) is a fundamental theory in explaining interrelationships among disturbance, plant diversity, and forest dynamics. The applicability of the theory of gap dynamics to natural forests has been hotly debated. In this commentary, results of empirical studies of tropical cyclone disturbance at the Fushan Long-term Ecological Research site are used to illustrate key limitations of the theory of gap dynamics and reveal previously overlooked processes that are essential to the disturbance-biodiversity-forest dynamics relationships.

Rethinking the theory of gap dynamics

The theory of gap dynamics emphasizes the role of canopy gaps created by tree-fall disturbances in initiating the forest cycle and spatial mosaics of structural phases that change over time (Whitmore 1989). Gaps are defined as openings in the forest canopy which help maintain species diversity through initiating new tree age classes and accelerating the growth of previously suppressed individuals under gaps (Whitmore 1989, Chandrashekara and Ramakrishnan 1994, Schnitzer and Carson 2001). Compared to the non-gap understory, light availability under canopy gaps is high, allowing the establishment and growth of shade-intolerant (or pioneer) tree seedlings and promoting the growth of small trees (Whitmore 1989). Moreover, when gaps are large, heterogeneity of light availability in gaps can be high enough to maintain the coexistence of shade-tolerant (late successional) and -intolerant species within the gap (Schnitzer and Carson 2001, McEwan et al. 2014). Therefore, gap dynamics associated with small-scale tree-fall disturbances are considered important and even essential for tree recruitment and diversity, and forest regeneration.

However, empirical studies of gap dynamics in relation to typhoon disturbances at the Fushan Long-term Ecological Research site indicate that the implicit fundamental assumption of contrasting environments between gap and non-gap sites of the theory of gap dynamics is circumstantial. The assumption is fundamental because contrasting environments of gaps and non-gap microsites respectively favor shade-intolerant and -tolerant species. The effects of gaps in maintaining or promoting species richness are mostly evident when many species establish only in gaps, because without gaps such species (mostly shade-intolerant pioneer species) cannot persist in the forest understory. However, in forests with annual typhoon disturbances such as the Fushan forest and those in low-elevation mountains of Taiwan, canopy gaps are generally small (e.g., with a mean of 10 m^2 and the largest of 36.4 m^2, Yao et al. 2015), due to the lack of many large trees and low typhoon-induced mortality (Mabry et al. 1998, Lin et al. 2011), compared to mature temperate and tropical forests (e.g., with a mean of 200 m^2 in many tropical forests, McCarthy 2001). In addition, the light availability in non-gap microsites is often > 10% of levels in the open due to frequent canopy disruptions associated with typhoons (Lin et al. 2003, Yao et al. 2015), compared to < 5% in most mature tropical and temperate forests (Canham et al. 1990). As a result of substantive annual canopy disruptions, light availability in non-gap microsites is high and does not differ from that of small gaps (Yao et al. 2015). Therefore, shade-intolerant species do not require canopy gaps for regeneration. Trees, both shade-tolerant and -intolerant, can survive and grow in both gaps and in the non-gap understory (Lin 2007), so that there are no significant differences in plant diversity or community compositions between gaps and non-gap microsites (Yao et al. 2015). In fact, at the Fushan Experimental Forest, all seedling species found under canopy gaps were found in the forest understory, but not all species in the forest understory were found in canopy gaps (Yao et al. 2015). In this regard, the statement that (some) “pioneer species establish only in gaps” as described by Molino and Sabatier (2001) could be misleading, because establishment of species depends on the environmental conditions not the status of the gap versus non-gap understory.

Frequent typhoons create gaps and obscure differences between gap and non-gap microsites, so that instead of being indispensable for the establishment of shade-intolerant species and contributing to overall tree diversity as described in the theory of gap dynamics, gaps may play a neutral role in plant diversity. Tree species do differ in their shade-tolerance, so that it is the availability and variability of light that are most important for determining the niches available for plants. The size and number of gaps could be in some cases good surrogates for light availability and variability, but that is not universal. Focusing on the surrogate instead of the actual factors could be misleading because the validity of the surrogate is often conditional.

Frequent typhoon disturbances are not the only disturbance that can obscure the distinction between gap and non-gap microsites. Canopy defoliation caused by insect outbreaks can also reduce foliar cover and increase canopy light penetration without creating "gaps". Canopy pruning commonly applied in forest plantation management has similar effects of reducing differences between gap and non-gap microsites. Ice storms can cause large losses of the canopy leaf area index but not necessary high tree mortality (Rhoads et al. 2002). Tropical cyclone intensity and frequency are projected to increase in the future (Walsh and Ryan 2000, Emanuel 2005, 2013, Webster et al. 2005, Elsner et al. 2008, Pun et al. 2013, Chand et al. 2017), so that obscured differences in gaps and non-gap microsites caused by frequent cyclones could become more common. In addition, climate change was suggested to have increased the extent and severity of insect outbreaks in North America (Kurz et al. 2008). Warmer winter temperatures in the northern hemisphere were suggested as being an important factor associated with forest defoliation caused by insect outbreaks (Neuvonen et al. 1999). These changes all have the potential to obscure differences in physical environments between gaps and non-gap microsites and invalidate the implicit assumption of the theory of gap dynamics.

CONCLUSIONS

The theory of gap dynamics provides generalizations about disturbance-diversity-forest dynamics relationships and is intuitively easy to comprehend. Such generalizations simplify the processes that lead to disturbance-diversity-forest dynamics relationships in nature. However, the real world is often more complicated with many surprises that cannot be fully understood from simplified generalizations. In the era of climate change characterized by more-frequent climate extremes and natural disturbances, we should move beyond generalizations and directly address the processes that lead to observed disturbance-diversity relationships.

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