



Edge effects on soil seed banks and understory vegetation in subtropical and tropical forests in Yunnan, SW China

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ABSTRACT

Human-induced forest edges are common in many forest landscapes throughout the world. Forest management requires an understanding of their ecological consequences. This study addressed the responses of three ecological groups (non-forest species, secondary forest species and primary forest species) in edge soil seed banks and edge understory vegetation, and explored the relationship between the invasion of non-forest species in edge understory vegetation and the accumulation of their seeds in edge soil seed banks. The soil seed banks and understory vegetation were sampled along transects established at the edges of a continuous subtropical evergreen broad-leaved forest tract (*Lithocarpus xylocarpus* forest) bordering anthropogenic grasslands and three tropical seasonal rain forest fragments (*Shorea wantianshuae* forest) bordering fallows. Species composition in both soil seed banks and understory vegetation showed great difference among edge sites. In soil seed banks, the dominance (relative abundance and relative richness) of each ecological group did not change significantly along the edge to interior gradient. In understory vegetation, the invasion of non-forest species concentrated on the first several meters along the edge to interior gradient. The dominance of secondary forest species decreased with distance from the edge, while the dominance of primary forest species increased with distance from the edge. In forest edge zones, the invasion of a majority of non-forest species in understory vegetation lags behind the accumulation of their seeds in soil seed banks. Forest edges do not act as a good barrier for the penetration of non-forest species seeds. The lack of non-forest species in understory vegetation must then be due to conditions that are not appropriate for their establishment. Therefore, to prevent germination and survival of non-forest species further into the forest, management should focus on maintaining interior forest conditions.

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1. Introduction

Human-induced forest edges are common in many forest landscapes and are becoming an increasingly prominent landscape component throughout the world. Their ecological consequences have attracted much attention from ecologists and conservationists (Murcia, 1995; Gascon et al., 2000; Laurance et al., 2001; Ries et al., 2004; Harper et al., 2005). After edges are created, the abiotic effects, direct and indirect biological effects are together termed as “edge effects” (Murcia, 1995). The negative edge effects on forest ecosystems are now widely recognized, such as structural damage (Williams-Linera, 1990; Lopez de Casenave et al., 1995; Ferreira and Laurance, 1997; Laurance et al., 1998), alien plant invasion (Saunders et al., 1991; Brothers and Spingarn, 1992; Pauchard and Alaback, 2006), and loss of biodiversity (Gascon et al., 2000; Laurance et al., 2002; Harper et al., 2005). Forest

management requires an understanding of these negative ecological consequences.

It is recognized that species respond to the habitat edge in a variety of patterns due to variable mechanisms (Ries and Sisk, 2004; Ries et al., 2004). Many studies have focused on groups of species that make up the edge community. Alien plant species (Brothers and Spingarn, 1992; Fraver, 1994; Rose and Fairweather, 1997; Goldblum and Beatty, 1999; King and Buckney, 2001), colonizing plants (Fox et al., 1997), weedy plant species (Honnay et al., 2002), disturbance-tolerant forest species (Gehlhausen et al., 2000) and pioneer and secondary forest tree species (Oosterhoorn and Kappelle, 2000) tend to become more common in forest edges. It has also been revealed that the strength of this positive feedback declined with increasing distance from the forest edge into the forest interior. Among these positive responses of plant species to the forest edge, the invasion of non-forest species is one of the most negative ecological consequences.

Seed availability is an important limiting factor for the invasion of alien species (King and Buckney, 2001; Pauchard and Alaback, 2006), invasive species (Cadenasso and Pickett, 2001) and

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competitive species (Devlaeminck et al., 2005) in forest edge zones. The forest edge is recognized as a potential starting point for invasion in forest ecosystem (Cadenasso and Pickett, 2001; Borgmann and Rodewald, 2005; Pauchard and Alaback, 2006). It is increased wind due to edge structural damage that will disperse external seeds further into forest. The significant changes of plant composition in understory vegetation at forest edges could occur over a few years to decades after edge creation (Matlack, 1994; Meiners and Pickett, 1999; Harper and Macdonald, 2002), which might be attributed to the long-term accumulation of external seeds at forest edges.

We have found that the invasion of non-forest species in understory vegetation lags behind that in soil seed banks in the forest interior (>200 m into the forest from the edge) (Lin et al., 2006). However, for the forest edge, we still do not know the contrasting response of non-forest species in soil seed banks and understory vegetation. In this study, we selected relatively old artificial forest edges from a continuous subtropical evergreen broad-leaved forest tract and three tropical seasonal rainforest fragments in Yunnan, SW China, to study the plant species responses to the forest edge in soil seed banks and understory vegetation. These two forest types are distributed in different climatic zones and therefore are very different in community structure and species composition (CGVY, 1987). The following question guided our research: Do the responses of the three ecological groups (non-forest species, secondary forest species and primary forest species) to the forest edge in soil seed banks differ from those in understory vegetation? Especially, we focused on whether or not the invasion of non-forest species in understory vegetation lags behind the accumulation of their seeds in soil seed banks in forest edge zones?

We categorized plant species occurring in a natural forest landscape as non-forest species (from surrounding landscapes and not part of the natural successional stages for our studied forest types), secondary forest species (natural constituent species for our studied forest types but occurring only in canopy gaps, forest edges and secondary forests) and primary forest species (natural

constituent species in mature stands of studied forest types) according to long-term monitoring of the dynamics in species composition of local forest succession (both primary forests and secondary forests). Non-forest species are species growing in habitats different from closed forests or their successional communities and usually include native and non-native weeds and plants that have escaped from cultivation (Lin et al., 2006). In this study, we used this categorization to explore the general pattern of plant species responses to the forest edge.

2. Methods

2.1. Study sites

One of our two study areas is located in the Xujiaba area (24°32'N, 101°01'E) on the northern crest (2400–2600 m) of Ailao Mountains in west-central Yunnan, SW China (Fig. 1). About 78% of the Xujiaba area (3700 ha) is covered continuously by mid-mountain moist evergreen broad-leaved forests. *Lithocarpus xylocarpus* forest is representative of the mid-mountain moist evergreen broad-leaved forest in this study area. The soil order is alfisols (Soil Survey Staff, 2003). Mean annual temperature is 11.3 °C and mean annual rainfall is 1931.1 mm, more than 85% of which falls from May to October (Data from Ailaoshan Station for Forest Ecosystem Studies). Outside this continuous forest tract, most of the natural vegetation has been converted to maize, sugarcane (low altitude) and paddy rice fields in basins. This continuous forest tract has been strictly protected as a part of the Ailao Mountain Nature Reserve since 1981. Thus, there remain many old forest edges originated from conversion to plantations, some of which have been abandoned as they are included into the region of Nature Reserve. However, so far, the abandoned fields still exist in the early successional stage of grassland because grazing and trampling cannot be prevented.

The other study area is located in Bubeng area (21°36'N, 101°34'E) in Xishuangbanna of Southern Yunnan, SW China (Fig. 1). There are *Shorea wantianshuela* forests (tropical seasonal

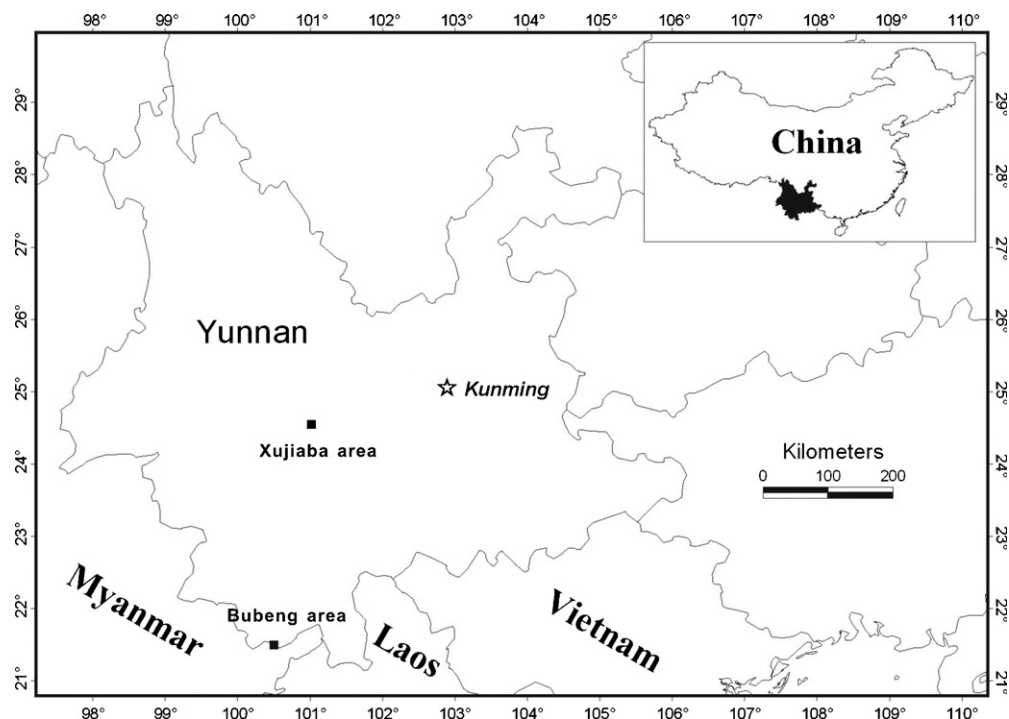


Fig. 1. Geographical locations of the two study areas in Yunnan Province, SW China.

Table 1
The characteristics of forest edge sites.

Study area and forest type	Site	Area of forest patch (ha)	Edge age (yr)	Geographical location		Elevation (m)	Edge aspect	Slope (°)
				Latitude	Longitude			
Xujiaba area, <i>Lithocarpus xylocarpus</i> forest	Xiaobazi	>3700	52	24°32'N	101°01'E	2440	SW	15
	Shanmenkounei	>3700	45	24°32'N	101°01'E	2440	W	10
	Shanmenkouwai	>3700	50	24°32'N	101°01'E	2240	S	20
Bubeng area, <i>Shorea wantianshuae</i> forest	Nanshahe	3	35	21°36'N	101°34'E	575	SE	10
	Huiduhe	20	10	21°36'N	101°34'E	610	SW	3
	Canopy walkway	5	10	21°37'N	101°35'E	433	W	25

rainforest) distributed but severely fragmented in this study area. The soil order is Oxisols (Soil Survey Staff, 2003). Mean annual temperature is 21 °C, and mean annual rainfall is 1500–1600 mm, about 83% of which falls from May to October. During the dry season, however, fog drip is an important input of water to this seasonal rainforest (Liu et al., 2004). *Shorea wantianshuae* forests in this study area have been isolated in many small fragments by cultivated lands. The species composition of the two forest types is well documented in CGVY (1987).

We used the following criteria for edge selection. (1) Forest edges must be abrupt and in similar orientations. (2) Forest edges must have relatively flat slopes and have enough width for the placement of three transects at more than 20 m intervals. (3) The landscapes outside forest edges are the same in nature and are created by the same human activity. We selected three edges for each forest type according to these criteria which could control some factors influencing edge responses, such as edge orientation and landscape type outside forest edges (Table 1).

2.2. Sampling understory vegetation

At each of the selected edges, we established three transects perpendicular to the edge boundary that was identified by canopy dripline. The three transects were separated by at least 20 m. Along each transect, we established 60 (*Lithocarpus xylocarpus* forest) or 50 (*Shorea wantianshuae* forest) contiguous 1 m × 1 m quadrats from the edge into the forest to investigate the species composition of understory vegetation. We also set up one quadrat at each of the distances of 5 m and 10 m outside forest edges along each transect to investigate the species composition of grasslands and fallows adjacent to forest edges.

Sampling was conducted from June through July 2005 for *Lithocarpus xylocarpus* forest and from August through October, 2005 for *Shorea wantianshuae* forest. Within each quadrat, we identified all vascular plant species up to 150 cm high and counted the number of individuals of each species. A clump of ramets of one clonal species was defined as a single "individual". Nomenclature follows Editorial Committee of Flora Reipublicae Popularis Sinicae (1959–2004).

2.3. Sampling soil seed banks and seed germination

We took soil samples of 10 cm × 10 cm × 10 cm at the distances of 5 m outside forest edges and 0 m, 5 m, 10 m, 20 m and 50 m inside forest edges along the transects established for understory vegetation investigation both in late rainy season (November 2004) and in late dry season (May 2005). Thus, there were 54 samples (each site had 18 samples) in each sampling time. The second sample in May was taken at 0.5 m from the first.

Before sampling, fresh litter on the soil surface was removed. The soil samples were separately placed in cloth bags and transported to a non-temperature controlled glasshouse in Xishuangbanna Tropical Botanical Garden for germination testing within 2 days of

collection. Each soil sample was spread to a depth of 1 cm in separate germination trays in the glasshouse. Trays were watered twice a day to keep the soil moist. Emerging seedlings were counted every 2 days for 6 months (see Cao et al., 2000), and those identified were removed with minimal disturbance to the soil. Seedlings that could not be identified were transplanted to pots at 6 months and grown to the flowering stage for identification to species. Soil samples were stirred in the fourth month of the experiment. Six control trays filled with sterilized soil were interspersed among the trays containing soil samples to detect potential contaminant seeds from the glasshouse environment. Only angiosperm taxa were considered. Nomenclature follows Editorial Committee of Flora Reipublicae Popularis Sinicae (1959–2004).

2.4. Data analysis

Patterns of species composition in understory vegetation were obtained by arbitrarily dividing each transect into plots (1 m × 5 m). Each plot consisted of five contiguous quadrats (1 m × 1 m).

Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) was used to explore the general pattern of species composition in understory vegetation and soil seed banks across forest edges. We ordinated 90 (*Shorea wantianshuae* forest) or 108 (*Lithocarpus xylocarpus* forest) plots of understory vegetation and 54 samples of soil seed banks in each sampling time based on species abundance data (number of individuals in each species in plots). Prior to the DCA, square root transformations were performed on species abundance data to dampen the effects of dominant species. Those species occurring in less than three plots or samples were not taken into analysis.

To quantify the changes of the dominance of each ecological group (non-forest species, secondary forest species and primary forest species) in soil seed banks and understory vegetation across forest edges, we determined the relative abundance (number of individuals in an ecological group/total number of individuals), and the relative richness (number of species in an ecological group/total number of species) in each plot.

An analysis of variance (ANOVA) of generalized linear models (GLM) was used to test for significance of the effects of edge site and distance from the forest edge on DCA plot scores and DCA soil sample scores. There are twelve distances: 0–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, 25–30 m, 30–35 m, 35–40 m, 40–45 m, 45–50 m, 50–55 m and 55–60 m at *Lithocarpus xylocarpus* forest edges and ten distances: 0–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, 25–30 m, 30–35 m, 35–40 m, 40–45 m and 45–50 m at *Shorea wantianshuae* forest edges for DCA plot scores. There are five distances: 0 m, 5 m, 10 m, 20 m and 50 m for DCA soil sample scores. Prior to analysis, the data of response variables were square root transformed to improve normality and stabilize variances of response variables.

Different methods have been used to determine the depth of edge influence on forest vegetation (Williams-Linera, 1990; Chen

et al., 1992, 1995; Fraver, 1994; Fox et al., 1997; Laurance et al., 1998; Harper and Macdonald, 2001, 2002; Honnay et al., 2002; MacQuarrie and Lacroix, 2003). The methods and the results are varied depending on the concerned variables, ecosystems and edge ages.

We determined the inward limit of non-forest species (all non-forest species combined as one response unit) to evaluate the extent of its edge response in understory vegetation. In our study, the abundance (number of individuals) of non-forest species in quadrats gradually decreased to zero along the edge to interior gradient. We arbitrarily defined the inward limit as the point at which the abundance of non-forest species is 5% of the mean abundance of non-forest species in quadrats in adjacent grasslands or fallows. The non-forest species abundance in quadrats at each forest edge was plotted against distance from the edge for the three transects combined. After plotting, nonlinear regression techniques were used to fit the data to various associated models in order to find the best model with highest R^2 value. Ultimately, the following negative exponential models were selected for non-forest species abundance.

$$y = y_0 + a \times \exp(-bx) \quad (1)$$

where y is the abundance of non-forest species in quadrats, x is the distance from the forest edge, y_0 , a and b are the regression coefficients. The inward limits of non-forest species in understory vegetation are the distance at the intersection of the curve with 5% of the mean abundance of non-forest species in quadrats in adjacent grasslands or fallows.

3. Results

3.1. Species composition

In both forest types, the number of species in secondary forest species was relatively close between in soil seed banks and in understory vegetation. The number of species in primary forest species was the highest among the three ecological groups in edge understory vegetation but the lowest in soil seed banks. The number of species in non-forest species was much less in edge understory vegetation than that in edge soil seed banks (Table 2). Of these non-forest species, only 9 (*Lithocarpus xylocarpus* forest) and 8 (*Shorea wantianshunea* forest) non-forest species were found both in edge understory vegetation and in edge soil seed banks. 75% (*Lithocarpus xylocarpus* forest) and 84% (*Shorea wantianshunea* forest) of non-forest species found in soil seed banks were still not present in understory vegetation (see Appendices A and C in supplementary data for the complete species list of the three ecological groups in soil seed banks and Appendices B and D in understory vegetation).

Species composition showed great difference among edge sites whether in soil seed banks or in understory vegetation (Figs. 2 and 3). There were significant effects of distance from the edge on species composition in understory vegetation of *Lithocarpus xylocarpus* forest (Table 3). The significant difference between the 0–10 m edge zones and the further edge zones can be detected

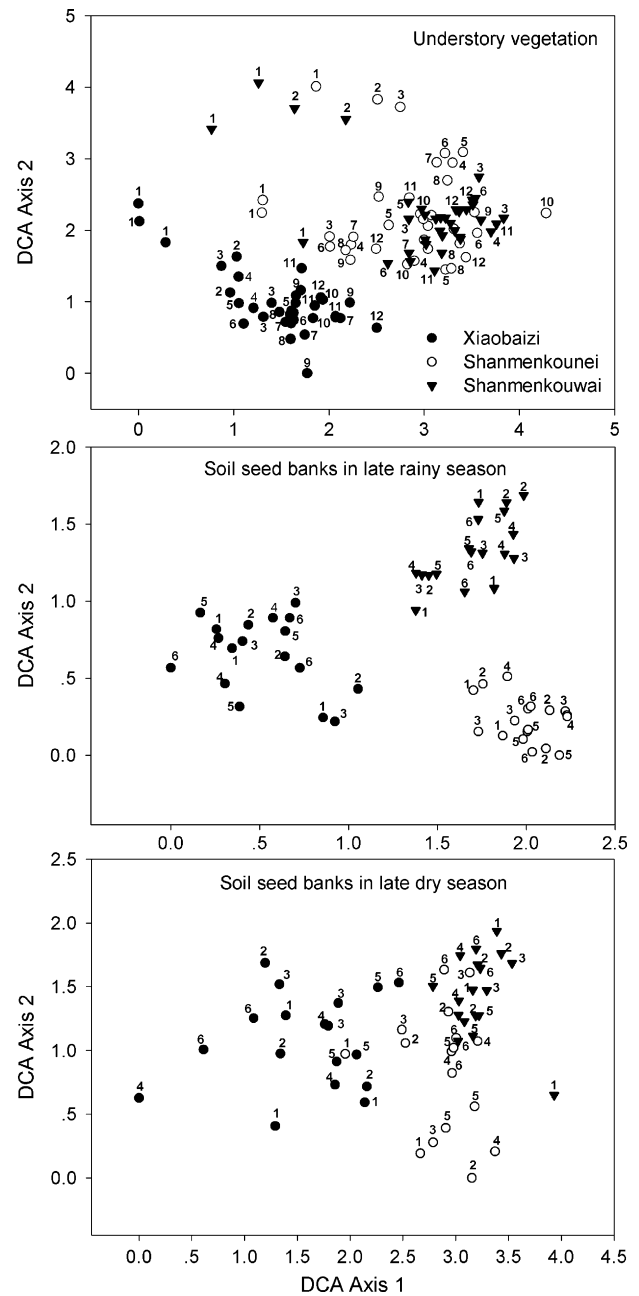


Fig. 2. DCA ordination diagrams for plots of understory vegetation, samples of soil seed banks in late rainy season and late dry season at the edges of *Lithocarpus xylocarpus* forest. The numbers near the symbols indicate the distance from the edge. For understory vegetation, 1: 0–5 m; 2: 5–10 m; 3: 10–15 m, 4: 15–20 m, 5: 20–25 m, 6: 25–30 m, 7: 30–35 m, 8: 35–40 m, 9: 40–45 m, 10: 45–50 m, 11: 50–55 m, 12: 55–60 m. For soil seed banks, 1: –10 m, 2: 0 m; 3: 5 m, 4: 10 m, 5: 20 m, 6: 50 m.

easily (Fig. 2). There were not significant effects of distance from the edge on species composition in understory vegetation of *Shorea wantianshunea* forest (Table 3). There were no effects of distance

Table 2

The number of species in each ecological group in both edge soil seed banks and edge understory vegetation for the two forest types.

Ecological group	<i>Lithocarpus xylocarpus</i> forest		<i>Shorea wantianshunea</i> forest	
	Soil seed banks (0–50 m)	Understory vegetation (0–60 m)	Soil seed banks (0–50 m)	Understory vegetation (0–50 m)
Non-forest species	36	18	50	20
Secondary forest species	61	48	73	76
Primary forest species	22	103	36	283
Others	1	5	6	14

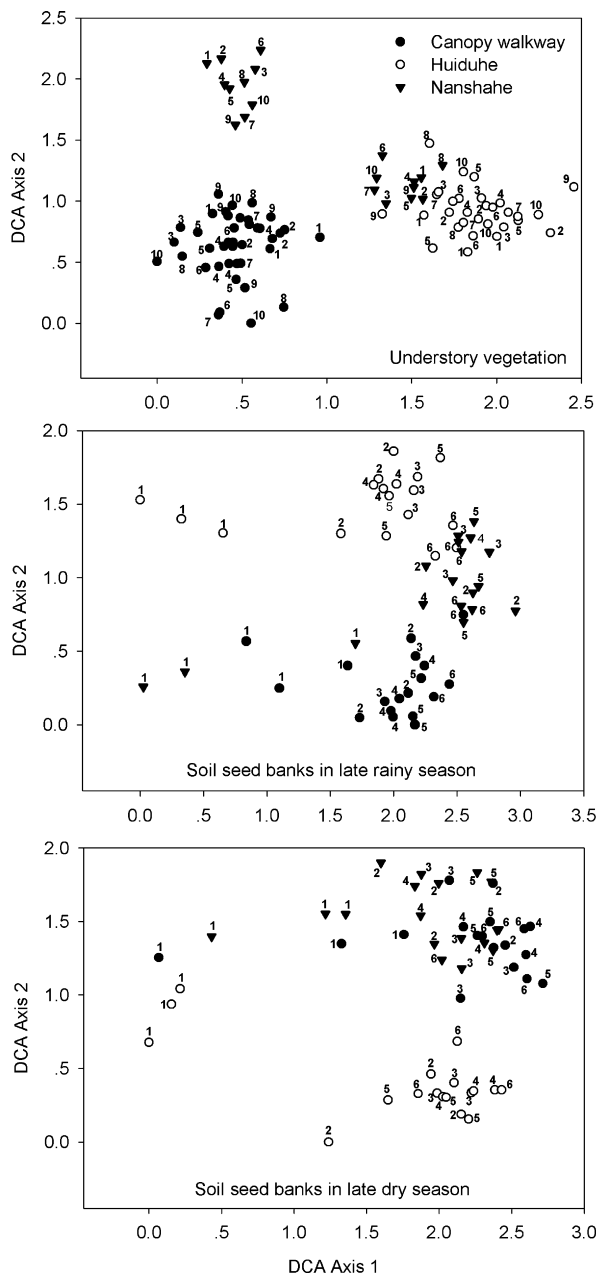


Fig. 3. DCA ordination diagrams for plots of understory vegetation, samples of soil seed banks in late rainy season and late dry season at the edges of *Shorea wantianshuea* forest. The numbers near the symbols indicate the distance from the edge (see Fig. 2).

from the edge on species composition in soil seed banks except that on DCA soil sample scores at axis 1 in late rainy season for *Shorea wantianshuea* forest (Table 3), which suggested that the species composition was relatively homogeneous in soil seed banks of forest edge zones (0–50 m).

3.2. Edge responses

In anthropogenic grasslands or fallows adjoining forest edges, secondary forest species and non-forest species dominated both in aboveground vegetation and in soil seed banks (Figs. 4 and 5).

In understory vegetation of both forest types, the degree of invasion by non-forest species was relatively high in 0–5 m edge zones and they disappeared in >5 m edge zones (Figs. 4 and 5). The inward limit of non-forest species in understory vegetation was

about 5 m and 1 m, respectively for *Lithocarpus xylocarpus* forest and for *Shorea wantianshuea* forest (Table 4). The dominance of secondary forest species sharply decreased in 0–15 m edge zones and remained low in >15 m edge zones, while the dominance of primary forest species sharply increased in 0–15 m edge zones and completely dominated in >15 m edge zones (Figs. 4 and 5).

In contrast, the relative abundance and relative richness of each ecological group did not change significantly along the edge to interior gradient (0–50 m) in soil seed banks whether in late rainy season or in late dry season (Figs. 4 and 5). Secondary forest species was always the most dominant ecological group in soil seed banks along the edge to interior gradient. The relative richness and relative abundance of non-forest species remained approximately 20–40% along the edge to interior gradient. Primary forest species remained relatively low dominance along the edge to interior gradient (Figs. 4 and 5).

4. Discussion

In both forest types, the invasion of a majority of non-forest species in understory vegetation lags behind the accumulation of their seeds in soil seed banks. Edge understory vegetation had changed in species composition, characteristic of invasion of non-forest species, proliferation of secondary forest species and decline of some primary forest species. The inward limit of non-forest species in understory vegetation in *Lithocarpus xylocarpus* forest is much greater than that in *Shorea wantianshuea* forest, which could be because *Lithocarpus xylocarpus* forest has older edges and lower species richness than *Shorea wantianshuea* forest.

Recently, ecologists have turned their attention from describing the edge structure and composition to exploring edge function (Fagan et al., 1999; Laurance et al., 2001; Cadenasso et al., 2003; Fagan et al., 2003). The permeability of edges to biotic and abiotic materials is often been focused (Wiens, 1992). Some studies reported that seeds that originated outside forests significantly decreased in amount both in seed rain and in soil seed banks along the edge to 50 m into forest (Cadenasso and Pickett, 2001; Devlaeminck et al., 2005). In this study, they did not decrease in the relative abundance with increasing distance from the edge to 50 m into forest (Figs. 4 and 5), and their relative abundance still accounted for 9.42% (Late rainy season) and 7.55% (Late dry season) in soil seed banks >200 m into forest in the same continuous forest tract in this study (Lin et al., 2006), which suggests that forest edges do not act as a good barrier for the penetration of non-forest species seeds. The relatively short sampling distance from the edge into the interior might be the reason for that we did not detect the declining trend in the amount of non-forest species seeds.

Given relatively great and homogeneous seed availability of non-forest species in our sampling forest edge zones, the short depth of penetration and abrupt decline in invasion degree of non-forest species in edge understory vegetation suggest that forest edges act as a barrier for the invasion of non-forest species to some extent. Taking the notorious invasive species, *Eupatorium adenophorum*, as example, its abundance in soil seed banks was relatively homogeneous along the edge to interior gradient, but its invasion in understory vegetation only concentrated in the 0–5 m edge zones (Fig. 6). Seed availability is not the major limiting factor for the invasion of non-forest species in forest edge zones. The lack of non-forest species in edge understory vegetation must then be due to conditions that are not appropriate for their establishment. Microenvironmental condition might be the major factor constraining the invasion of non-forest species in edge understory vegetation. Some abiotic limiting factors, such as light availability and soil chemistry, have been suggested by some studies (Brothers and Spingarn, 1992; Gehlhausen et al., 2000; Honnay et al., 2002). The pattern of changes in these abiotic factors across forest edges

Table 3
F value and significance of response variables in GLM ANOVA models.

Forest type	Response variable	Model ^a	Edge site ^b	Distance ^c	Edge site × distance
<i>Lithocarpus xylocarpus</i> forest	DCA plot scores at axis 1	16.717 ^{***}	155.690 ^{***}	21.068 ^{***}	1.908 [*]
	DCA plot scores at axis 2	5.899 ^{***}	78.093 ^{***}	3.548 ^{**}	0.961 NS
	DCA soil sample scores at axis 1 in late rainy season	12.909 ^{***}	86.700 ^{***}	0.538 NS	0.647 NS
	DCA soil sample scores at axis 2 in late rainy season	11.370 ^{***}	75.682 ^{***}	0.637 NS	0.658 NS
	DCA soil sample scores at axis 1 in late dry season	4.466 ^{**}	26.718 ^{***}	0.597 NS	0.838 NS
	DCA soil sample scores at axis 2 in late dry season	1.391 NS			
<i>Shorea wantianshuea</i> forest	DCA plot scores at axis 1	9.545 ^{***}	136.631 ^{***}	0.092 NS	0.126 NS
	DCA plot scores at axis 2	3.867 ^{***}	51.936 ^{***}	0.176 NS	0.360 NS
	DCA soil sample scores at axis 1 in late rainy season	8.020 ^{***}	35.793 ^{***}	6.125 ^{**}	2.025 NS
	DCA soil sample scores at axis 2 in late rainy season	14.211 ^{***}	94.248 ^{***}	0.462 NS	1.075 NS
	DCA soil sample scores at axis 1 in late dry season	2.525 [*]	9.466 ^{**}	2.053 NS	1.025 NS
	DCA soil sample scores at axis 2 in late dry season	18.863 ^{***}	126.500 ^{***}	0.160 NS	1.306 NS

NS: not significant.

^a Response = intercept + edge site + distance + edge site × distance.

^b There are three edge sites both for *Lithocarpus xylocarpus* forest and for *Shorea wantianshuea* forest (see Table 1).

^c There are twelve distances at *Lithocarpus xylocarpus* forest edges and ten distances at *Shorea wantianshuea* forest edges for DCA plot scores. There are five distances for DCA soil sample scores.

^{*} 0.01 ≤ P < 0.05.

^{**} 0.001 ≤ P < 0.01.

^{***} P < 0.001

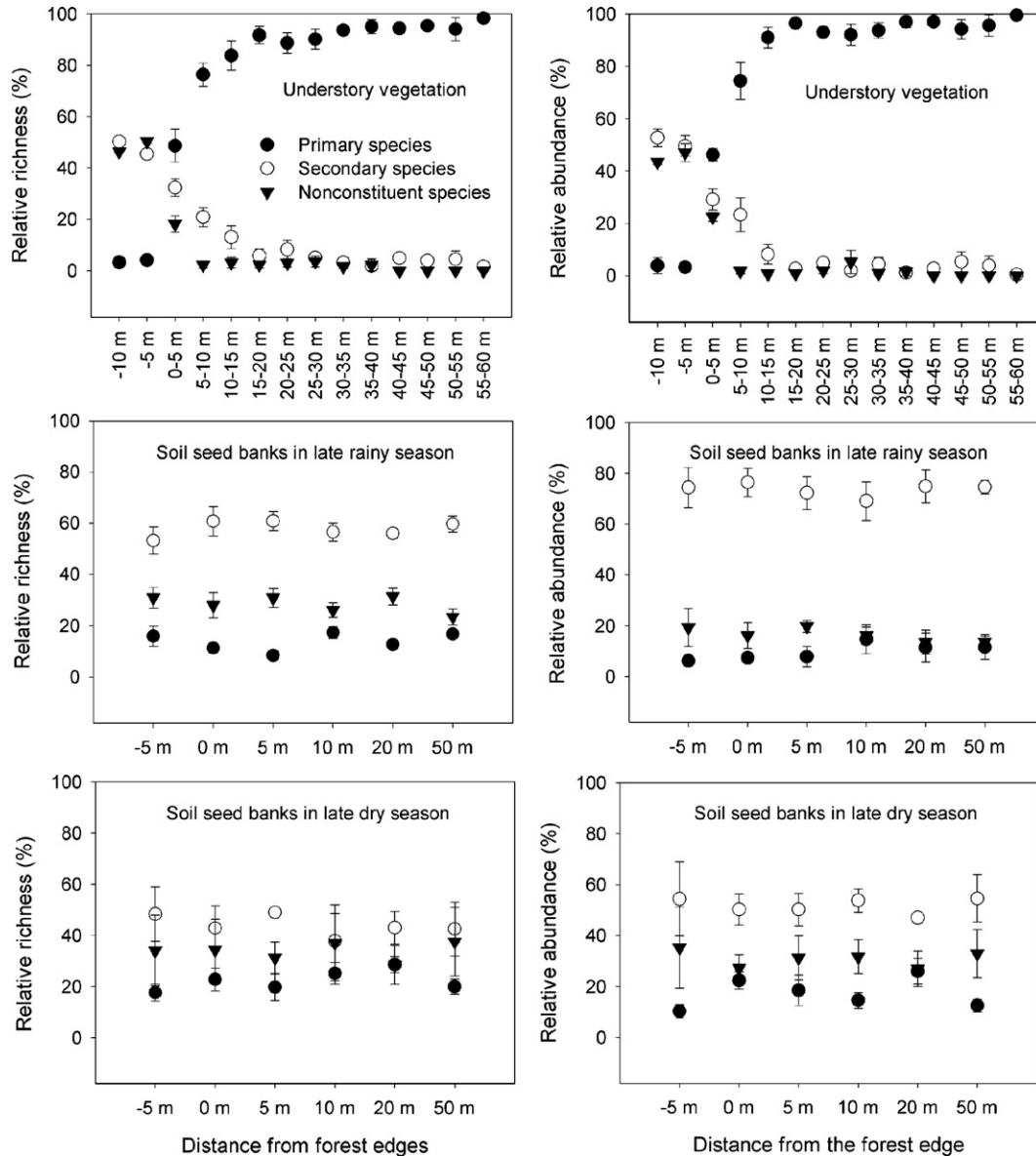


Fig. 4. The relative richness (Mean ± SE, n = 3) and relative abundance (Mean ± SE, n = 3) of each ecological groups in understory vegetation and soil seed banks in late rainy season and late dry season at the edges of *Lithocarpus xylocarpus* forest. Distances with negative signs were outside from the forest edge into the grassland.

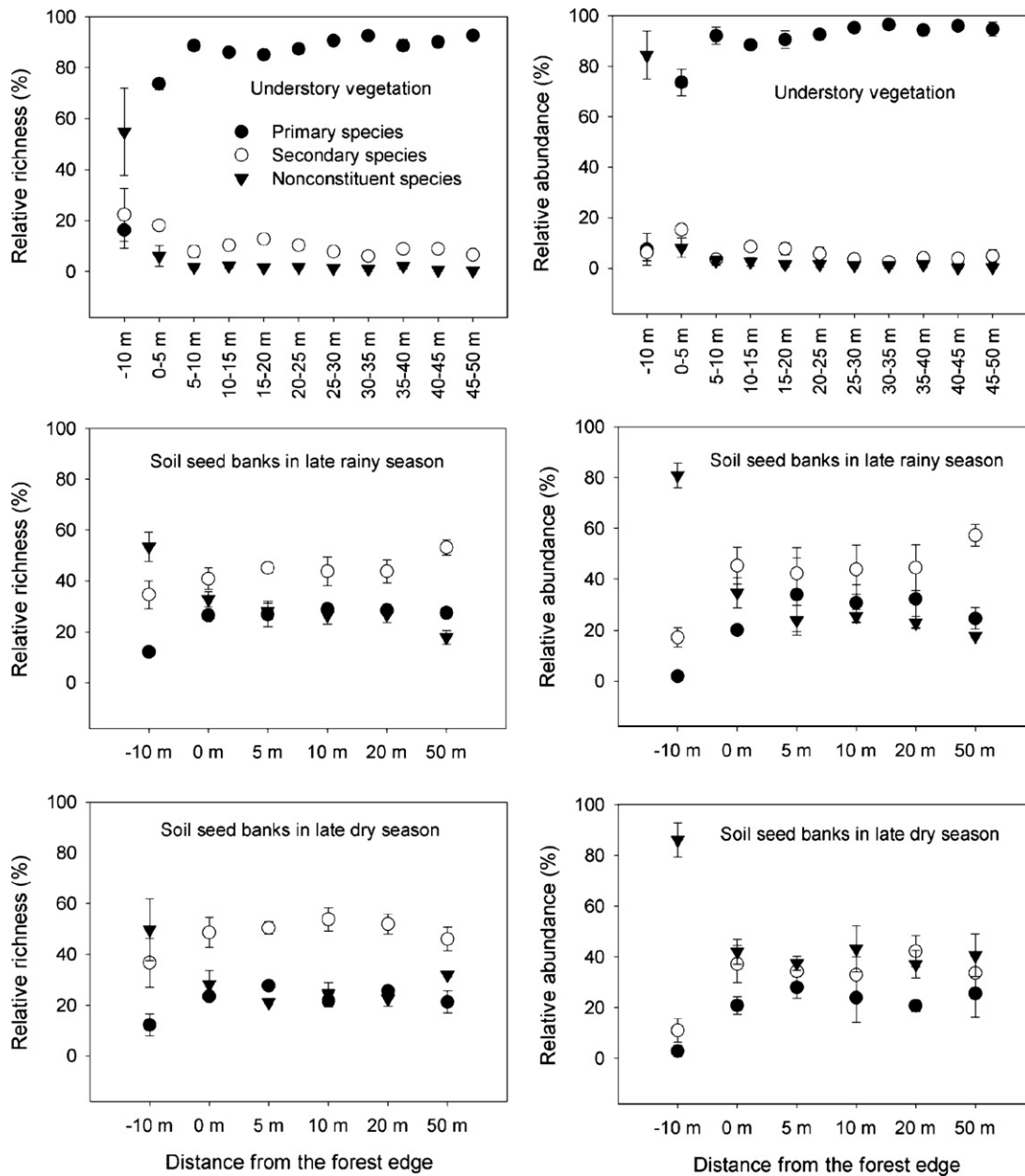


Fig. 5. The relative richness (Mean \pm SE, $n = 3$) and relative abundance (Mean \pm SE, $n = 3$) of each ecological groups in understory vegetation and soil seed banks in late rainy season and late dry season at the edges of *Shorea wantianshuea* forest. Distances with negative signs were outside from the forest edge into the fallow.

has a direct implication for the invasion process of weedy plant species (Honnay et al., 2002) and alien plant species (Brothers and Spingarn, 1992; Gehlhausen et al., 2000).

Although 9 (*Lithocarpus xylocarpus* forest) and 12 (*Shorea wantianshuea* forest) non-forest species occurring in understory

vegetation were not recorded in soil seed banks, which might result from that our soil samples did not include them, 27 (*Lithocarpus xylocarpus* forest) and 42 (*Shorea wantianshuea* forest) non-forest species found in soil seed banks were still not present in understory vegetation (See Appendices A and C in supplementary

Table 4
The inward limits of non-forest species in understory vegetation estimated by negative exponential models.

Forest type	Edge site	Fitted model	Mean abundance per quadrat outside edge (5% of mean) (ind./m ²)	Inward limit (m)
<i>Lithocarpus xylocarpus</i> forest	Xiaobazi	$y = 0.18 + 62.52 \exp(-0.50x)$, $R^2 = 0.72^{***}$	62 (3)	6
	Shanmenkounei	$y = 0.33 + 37.04 \exp(-0.59x)$, $R^2 = 0.55^{***}$	64 (3)	4
	Shanmenkouwai	$y = -0.08 + 30.60 \exp(-0.43x)$, $R^2 = 0.29^{***}$	67 (3)	5
<i>Shorea wantianshuea</i> forest ^a		$y = 0.32 + 112.30 \exp(-2.52x)$, $R^2 = 0.27^{***}$	95 (5)	1

^a The data from three edge sites (Nanshahe, Huiduhe, Canopy walkway) were pooled to fitted the model because the effect of edge site is not significant (two way ANOVA, $F = 0.560$, $P \geq 0.05$).
*** $P < 0.001$.

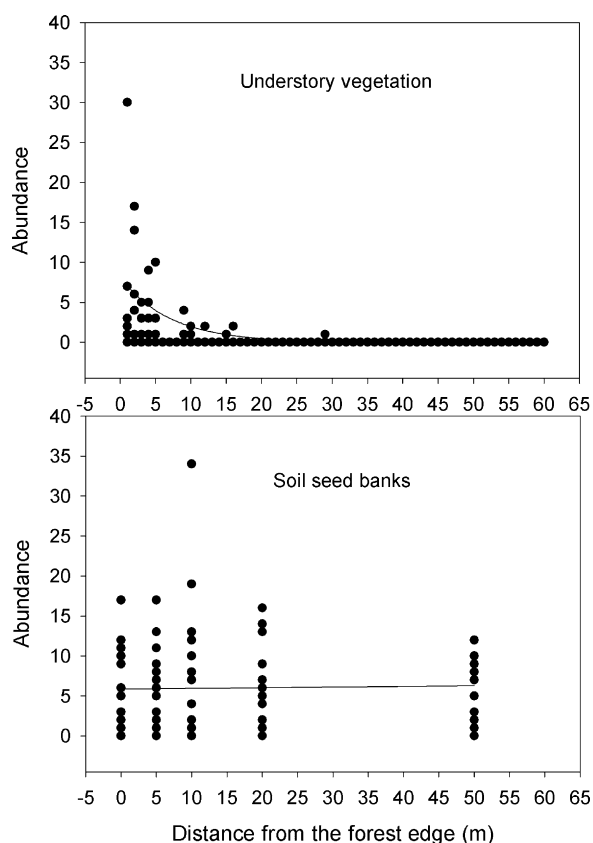


Fig. 6. The abundance of *Eupatorium adenophorum* in understory vegetation and soil seed banks along the edge to interior gradient in *Lithocarpus xylocarpus* forest.

data). However, the potential of invasion is great for those non-forest species which have accumulated abundant seeds in soil seed banks. For example, the notorious invasive species, *Eupatorium adenophorum* was the most abundant non-forest species both in soil seed banks and in understory vegetation in *Lithocarpus xylocarpus* forest edge zones. A native weed, *Thysanolaena maxima*, was the most dominant (relative abundance, 9.87%) species in soil seed banks in *Shorea wantianshuae* forest edge zones, and was also dominant in soil seed banks in a seasonal rainforest fragment interior (Cao et al., 2000). Although it was not found in understory vegetation, it could dominate secondary grasslands that developed on lands where most woody plants were removed by human activity (Zhang and Cao, 1995). Thus, the status of non-forest species in soil seed banks in forest edge zones is still able to provide early signal of invasion in aboveground vegetation as well as in forest interiors which have been suggested by Lin et al. (2006). Due to predictive function of soil seed banks for invasion of non-forest species in forest edge ecosystems, the soil seed bank should be a key item in monitoring and assessment programs for forest health and integrity.

Some studies have showed that increased disturbances can promote invasion in further distance from the forest edge (Laurance, 1991; Laurance, 2000; Peter, 2001). Human disturbance often induces structural damage and microenvironmental conditions change at forest edges, which could promote non-forest species to establish further into the forest. Didham and Lawton (1999) reported that edge penetration distances of most variables of microclimate and vegetation structure at open edges were 2–5 times greater than those at closed edges. The most effective approach to prevent germination and survival of non-forest species further into the forest is to forbid direct human disturbance, such as cutting and fire, to accelerate the edge

sealing which could maintain interior forest conditions and stabilize the edge responses. It is also feasible to grow a native trees strip with a certain width adjoining edges of small forest fragments demanding urgent conservation, which will buffer the edge effects of microclimate (Denyer et al., 2006). Surrounding land uses can also influence invasion by exotic plants at forest edges (Borgmann and Rodewald, 2005). The adjacent heterogeneous landscape is an important source for non-forest species to invade forest edge zones. For example, there were 78% of non-forest species in understory vegetation and 28% of non-forest species in soil seed banks of forest edge zones also found in grasslands adjacent to *Lithocarpus xylocarpus* forest edges. Forest managers should convert previous deleterious land uses outside the forest to less deleterious or favored ones.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.12.004.

References

- Borgmann, K.L., Rodewald, A.D., 2005. Forest restoration in urbanizing landscapes: interactions between land uses and an exotic shrub. *Restoration Ecology* 13, 334–340.
- Brothers, T.S., Spingarn, A., 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* 6, 91–100.
- Cadenasso, M.L., Pickett, S.T.A., 2001. Effect of edge structure on the flux of species into forest interiors. *Conservation Biology* 15, 91–97.
- Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., Jones, C.G., 2003. A framework for a theory of ecological boundaries. *Bioscience* 53, 750–758.
- Cao, M., Tang, Y., Sheng, C.Y., Zhang, J.H., 2000. Viable seeds buried in the tropical forest soils of Xishuangbanna, SW China. *Seed Science Research* 10, 255–264.
- Chen, J., Franklin, J.F., Spies, T.A., 1992. Vegetation responses to edge environments in old-growth Douglas-Fir forests. *Ecological Applications* 2, 387–396.
- Chen, J., Franklin, J.F., Spies, T.A., 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5, 74–86.
- Compiling Group of the Vegetation of Yunnan, 1987. *The Vegetation of Yunnan*. Science Press, Beijing (in Chinese).
- Denyer, K., Burns, B., Ogden, J., 2006. Buffering of native forest edge microclimate by adjoining tree plantations. *Austral Ecology* 31, 478–489.
- Devlaeminck, R., Bossuyt, B., Hermy, M., 2005. Inflow of seeds through the forest edge: evidence from seed bank and vegetation patterns. *Plant Ecology* 176, 1–17.
- Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31, 17–30.
- Editorial Committee of Flora Reipublicae Popularis Sinicae, 1959–2004. *Flora Reipublicae Popularis Sinicae*. Sciences Press, Beijing (in Chinese).
- Fagan, W.F., Cantrell, R.S., Cosner, C., 1999. How habitat edges change species interactions. *American Naturalist* 153, 165–182.
- Fagan, W.F., Fortin, M.-J., Soykan, C., 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *Bioscience* 53, 730–738.
- Ferreira, L.V., Laurance, W.F., 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. *Conservation Biology* 11, 797–801.
- Fox, B.J., Taylor, J.E., Fox, M.D., Williams, C., 1997. Vegetation changes across edges of rainforest remnants. *Biological Conservation* 82, 1–13.

- Fraver, S., 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. *Conservation Biology* 8, 822–832.
- Gascon, C., Williamson, G.B., da Fonseca, G.A.B., 2000. Receding forest edges and vanishing reserves. *Science* 288, 1356–1358.
- Gehlhausen, S.M., Schwartz, M.W., Augspurger, C.K., 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* 147, 21–35.
- Goldblum, D., Beatty, S.W., 1999. Influence of an old field/forest edge on a north-eastern United States deciduous forest understory community. *Journal of the Torrey Botanical Society* 126, 335–343.
- Harper, K.A., Macdonald, S.E., 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. *Ecology* 82, 649–659.
- Harper, K.A., Macdonald, S.E., 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. *Journal of Vegetation Science* 13, 535–546.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brososke, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaitoh, M.S., Esseen, P.-A., 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19, 768–782.
- Hill, M.O., Gauch Jr., H.G., 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42, 47–58.
- Honnay, O., Verheyen, K., Hermy, M., 2002. Permeability of ancient forest edges for weedy plant species invasion. *Forest Ecology and Management* 161, 109–122.
- King, S.A., Buckney, R.T., 2001. Exotic plants in the soil-stored seed bank of urban bushland. *Australian Journal of Botany* 49, 717–720.
- Laurance, W.F., 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. *Biological Conservation* 57, 205–219.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance, S.G., 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79, 2032–2040.
- Laurance, W.F., 2000. Do edge effects occur over large spatial scales? *Trends in Ecology and Evolution* 15, 134–135.
- Laurance, W.F., Didham, R.K., Power, M.E., 2001. Ecological boundaries: a search for synthesis. *Trends in Ecology and Evolution* 16, 70–71.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16, 605–618.
- Lin, L., Cao, M., He, Y., Baskin, J.M., Baskin, C.C., 2006. Nonconstituent species in soil seed banks as indicators of anthropogenic disturbance in forest fragments. *Canadian Journal of Forest Research* 36, 2300–2316.
- Liu, W., Meng, F.R., Zhang, Y., Liu, Y., Li, H., 2004. Water input from fog drip in the tropical seasonal rain forest of Xishuangbanna, South-West China. *Journal of Tropical Ecology* 20, 517–524.
- Lopez de Casenave, J., Pelotto, J.P., Protomastro, J., 1995. Edge-interior differences in vegetation structure and composition in a Chaco semi-arid forest, Argentina. *Forest Ecology and Management* 72, 61–69.
- MacQuarrie, K., Lacroix, C., 2003. The upland hardwood component of Prince Edward Island's remnant Acadian forest: determination of depth of edge and patterns of exotic plant invasion. *Canadian Journal of Botany* 81, 1113–1128.
- Matlack, G.R., 1994. Vegetation dynamics of the forest edge-trends in space and successional time. *Journal of Ecology* 82, 113–123.
- Meiners, S.J., Pickett, S.T.A., 1999. Changes in community and population responses across a forest-field gradient. *Ecography* 22, 261–267.
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10, 58–62.
- Oosterhoorn, M., Kappelle, M., 2000. Vegetation structure and composition along an interior-edge-exterior gradient in a Costa Rican montane cloud forest. *Forest Ecology and Management* 126, 291–307.
- Pauchard, A., Alaback, P.B., 2006. Edge type defines alien plant species along *Pinus contorta* burned, highway and clearcut forest edges. *Forest Ecology and Management* 223, 327–335.
- Peter, H.A., 2001. *Clidemia hirta* invasion at the Pasoh forest reserve: an unexpected plant invasion in an undisturbed tropical forest. *Biotropica* 33, 60–68.
- Ries, L., Sisk, T.D., 2004. A predictive model of edge effects. *Ecology* 85, 2917–2926.
- Ries, L., Fletcher Jr., R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution and Systematics* 35, 491–522.
- Rose, S., Fairweather, P.G., 1997. Changes in floristic composition of urban bushland invaded by *Pittosporum undulatum* in northern Sydney, Australia. *Australian Journal of Botany* 45, 123–149.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5, 18–32.
- Soil Survey Staff, 2003. *Keys to Soil Taxonomy*, 9th ed. U.S. Department of Agriculture and Natural Resources Conservation Service, Washington, DC.
- Wiens, J.A., 1992. Ecological flows across landscape boundaries: a conceptual overview. In: Hansen, A.J., di Castri, F. (Eds.), *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer-Verlag, New York, pp. 217–235.
- Williams-Linera, G., 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78, 356–373.
- Zhang, J.H., Cao, M., 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biological Conservation* 73, 229–238.