

Regeneration pattern of primary forest species across forest-field gradients in the subtropical Mountains of Southwestern China

Xiao-Shuang Li · Wen-Yao Liu · Jun-Wen Chen ·
Cindy Q. Tang · Chun-Ming Yuan

Received: 29 October 2009 / Accepted: 7 February 2010 / Published online: 13 April 2010
© The Botanical Society of Japan and Springer 2010

Abstract Evergreen broad-leaved forest is now gradually degraded and fragmented, and there is an increase in the amount of habitat edges as a result of long-term human activity. However, the role of edges in the regeneration of primary forest species is poorly understood. After 20 years of the edge creation, we analyzed primary forest species distribution and abundance, and changes in floristic composition, vegetation structure across forest-field gradients in Ailao Mountain, SW China. Our results revealed that there was a higher abundance and richness of primary species, late secondary species and thorny lianas at the distances 0–50 m than at the distances more than 50 m from the edge into the forest exterior. At the distances >50 m, no individuals of dominant canopy trees *Lithocarpus xylocarpus*, *Castanopsis wattii*, and *L. jingdong-*

ensis were found, whereas the abundance of early pioneer shrub species and herbaceous cover was significantly greater. The richness of primary species showed a decrease with increasing distances from the forest edge to the exterior, particularly of medium-seeded primary species showing a drastic decrease. Moreover, no large-seeded primary species occurred at the distances >60 m. This study indicates that the forest edge as a buffer zone may be in favor of primary species regeneration. A dense shrub and herb layer, and seed dispersal may be the major factors limiting the forest regeneration farther from the forest edge. Therefore, to facilitate forest recovery processes, management should give priority to the protection of buffer zones of this forest edge.

Keywords Vegetation structure · Primary species · Forest edge · Regeneration · Evergreen broad-leaved forest

Electronic supplementary material The online version of this article (doi:10.1007/s10265-010-0326-5) contains supplementary material, which is available to authorized users.

X.-S. Li · W.-Y. Liu (✉)
Key Laboratory of Tropical Forest Ecology, Xishuangbanna
Tropical Botanical Garden, Chinese Academy of Sciences,
650223 Kunming, China
e-mail: liuw@xtbg.ac.cn

X.-S. Li
Graduate School of the Chinese Academy of Sciences,
100039 Beijing, China

W.-Y. Liu
School of Environmental Biology, Curtin University
of Technology, Perth, WA 6845, Australia

J.-W. Chen
Department of Crop Science, College of Agronomy
and Biotechnology, Yunnan Agricultural University,
650201 Kunming, China

C. Q. Tang
Institute of Ecology and Geobotany, Yunnan University,
650091 Kunming, China

C.-M. Yuan
Yunnan Academy of Forestry, 650204 Kunming, China

C.-M. Yuan
Yunnan Laboratory for Conservation of the Rare, Endangered
and Endemic Forest Plants, State Forestry Administration,
and Yunnan Key Laboratory for Forest Plant Cultivation
and Utilization, 650204 Kunming, China

Introduction

Evergreen broad-leaved forest is now recognized as an important global vegetation formation type (Wang et al. 2007). This type of forest dominated by the genera *Castanopsis*, *Lithocarpus*, and *Cyclobalanopsis* (Fagaceae), *Machilus* and *Persea* (Lauraceae), and *Schima* (Theaceae) is almost exclusively distributed throughout eastern Asia (Kira 1991; Tagawa 1995). However, as a result of long-term human activity, including deforestation, logging, fire and unsustainable agricultural practices, this forest is now degraded to tree plantations, secondary forests, shrublands, pasturelands, and croplands (Dickerman et al. 1981; Tanouchi and Yamamoto 1995; Zhu et al. 2009). These areas usually are prone to be overtaken by herbaceous plants and generalist plant species, and thus the natural re-colonization is very slow, e.g., *Lithocarpus xylocarpus*, *Castanopsis wattii*, and *L. jingdongensis*.

The ability of forest species to establish in the open fields depends on the ability of its seeds to disperse, to germinate, to compete and to survive (Cavallin and Vasseur 2008). However, when forests are destroyed, abrupt shifts in vegetation structure and floristic composition cause environmental conditions to change substantially along the forest-field gradients (Williams-Linera 1990). As compared with forest interior, the forest outside receives more light, and has higher air and soil temperature, lower relative humidity and soil moisture, and also encounters wind shear forces (Jose et al. 1996; Laurance 1997; Didham and Lawton 1999). In response to these changes in abiotic conditions, shrub stem densities, herb cover, and exotic plant species near the forest edge are higher than those in the forest interior (Williams-Linera et al. 1998; Didham and Lawton 1999; Gehlhausen et al. 2000). A combination of the above factors may result in poor tree seedling survival and growth. In addition, degraded areas could expose animal seed dispersers to predators and have no perches or fruits, which may thus negatively affect seed dispersal in large-seeded plant species that depend on these animals for dispersal (Howe and Smallwood 1982; Godínez-Álvarez et al. 2002).

It has been widely documented that forest fragmentation resulted from deforestation and disturbance leads to a greater abundance and richness of secondary species and exotic plant species near fragmented edges (Laurance 1991; Williams-Linera et al. 1998; Laurance et al. 2001), particularly of thorny and prickly species (Pandey and Shukla 2003). For example, Bakker et al. (2004) reported that temperate woodlands and meadows supported a variety of thorny species that occurred mostly along forest edges. Hill and Wallace (1989) found that the forest edge was notably thorny, with 42 percent cover of *Rubus* because of disturbance at Newborough forest, Anglesey. Numerous studies have shown that thorny species facilitated forest regeneration in disturbed areas because of providing safe habitats for

the seedling and saplings from being browsed (Coops 1988; Olf et al. 1999). Acceptably, once the protection from the shrubs has disappeared, the trees would be unable to regenerate (Pandey and Shukla 2003; Tashi 2004).

Up to now, many previous studies about edge effects have mainly concentrated on effects of edges on microclimatic and vegetation patterns within the forest community (Williams-Linera 1990; Jose et al. 1996; Euskirchen et al. 2001), and negative effects of edges on forest ecosystems, such as structural damage and alien plant species invasions (Williams-Linera 1990; Ferreira and Laurance 1997; Lin and Cao 2009). However, relatively few have elucidated the regeneration of primary forest species, especially of dominant species, along an interior-edge-exterior gradient in relation to the subtropical evergreen broad-leaved forest area. The present study, therefore, aims at quantifying the spatial distribution of primary forest species along the forest-field gradients. Specific hypotheses were that the forest edge as a buffer zone which supported an abundance of thorny lianas could facilitate forest regeneration, and that a dense shrub and herb layer, and seed dispersal might be the major factors limiting the forest regeneration at sites far away from the forest edge.

Materials and methods

Study site

The study site is located in the Xujiaba region (2,000–2,650 m asl), a key area of the Ailao Mountain National

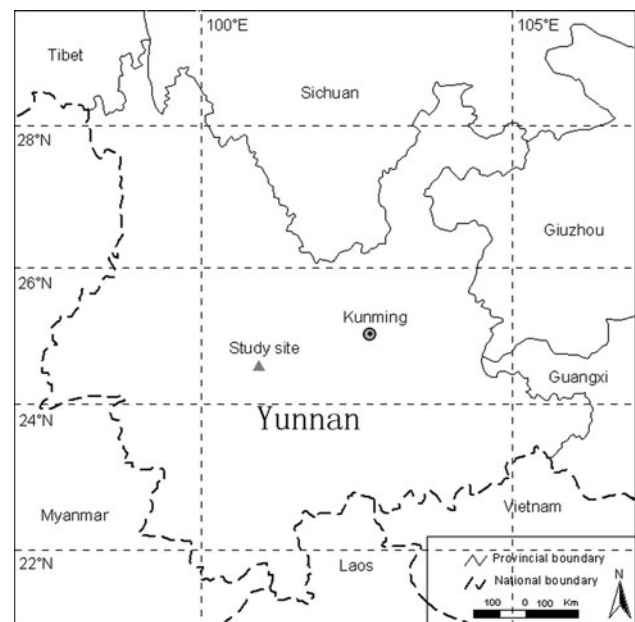


Fig. 1 Geographical location of the study site

Nature Reserve, covering 5,100 ha on the northern crest of the Ailao Mountains in south-central Yunnan (Fig. 1; 23°35'N–24°44'N, 100°54'E–101°30'E). Meteorological observations (1982–1992) at the Forest Ecosystem Research Station, Xujiaba (24°32'N, 101°01'E, 2,450 m asl) show an annual mean precipitation of 1,931.1 mm (85% in the rainy season from May to October). Annual evaporation is 1,485.5 mm (23% less than precipitation). Annual mean air temperature is 11.3°C (from 5.4°C in January to 16.4°C in July). The mean active accumulative temperature above 10°C is about 3,420°C, making this area similar to the warm temperate zone (Liu et al. 2002). Natural disturbances most commonly affecting forests in the Ailao Mountains are strong winds and the occasional cold spells that may be accompanied by snowfall. The soil under the evergreen broad-leaved forest is a typical yellow-brownish earth, with high organic matter and nitrogen content. The parent rock is mainly schist, gneiss, and diorite. The soil texture is loam, with acidic pH (4.2–4.6). The thickness of the litter layer covering almost all the soil surface is about 3–7 cm.

Natural vegetation consists of 18–25 m tall mid-montane moist evergreen broad-leaved forest, dominated by the species of *Castanopsis*, *Lithocarpus*, *Machillus*, and *Shima*. This primary forest is characterized by moist, shaded conditions, and a closed canopy (>90%). The subcanopy is estimated to have a cover of >50%. Shrub, bamboo, and ground cover herbs occur in localized patches. Various epiphytes, climbing plants, ferns, mosses on tree boles and branches, exposed rock and dead wood (Liu et al. 2002).

Since the early 1980s, local inhabitants had to abandon most agricultural fields because of establishing the Ailao Mountain National Nature Reserve. Nowadays, a diverse, multifaceted landscape mosaic was found, which includes different-aged secondary forest, successional shrubland, and pastureland in the frontier zone of the Reserve. This study site, which is a typical of agricultural area with a mosaic of different successional stages, is located in an about 30 ha abandoned agricultural field and closes to primary forest. The abandoned fields had been previously used to intensively grow corn, potatoes (*Solanum tuberosum* L.) and buckwheat (*Fagopyrum esculentum* Moench.) for over 20 years. Since abandoned in 1987, it was kept under natural succession without any disturbance, such as cultivation, cutting, grazing and fires. Study site age and land-use history were determined by the Management Authority of the Ailao Mountain Nature Reserve, Yunnan, and by questioning local inhabitants.

Sampling design and data collection

In April 2008, a total of four belt transects separated by about 50–100, 200 m in length and 10 m in width, were

established, running from the forest interior (–50 m) through the edge (0 m) to the exterior (i.e. field: 150 m), perpendicular to the forest edge. We defined the edge as a line coinciding with the bases of bordering mature (≥ 30 cm DBH, diameter at breast height) tree stems (Fraver 1994; Jose et al. 1996; Oosterhoorn and Kappelle 2000; López-Barrera 2003). Each transect was divided into 20 contiguous plots of 10 m \times 10 m. Five plots distributed over the forest interior, and fifteen plots distributed over the forest exterior. Sampling plot 1 to plot 20 are located at each transect from forest interior to exterior. Label as T1P1 (Transect 1–Plot 1), T1P2, T1P3, T4P1 (Transect 4–Plot 1), etc. All of transect were in the same successional stage, and were affected by the effects of same management.

From April to August 2008 (the end of dry season/middle of wet season) vegetation censuses were conducted in all 80 plots. This was done to ensure that the entire flora was considered. In each quadrat sampled in the belt transects, number, species name, DBH of all woody plants (including lianas), and heights (H) (measure using a clinometer) of woody shrubs and trees were recorded. Herbaceous plants were counted and recorded by species. We characterized all woody plants into the following size class: trees (stems ≥ 10 cm DBH), poles (stems ≥ 5 cm DBH and < 10 cm DBH), saplings (stems ≥ 1.3 m tall and < 5 cm DBH: stem diameter at 1.3 m), and seedlings (stems ≥ 0.2 m tall and < 1.3 m tall) (Mwima and McNeillage 2003).

Specimens were classified according to life form into tree, shrub, liana, and herb. We adapted the regeneration categories which were recorded in *List of Vascular Plant on Ailao Mountains Natural Reserve* (1996) by the Ailao Mountain Forest Ecosystem Research Station. The species encountered in the study site were categorized into three regeneration guilds: primary species (these species that could regenerate in the deep shade found under the closed canopy of these forests), late secondary species (these species are typically light-demanding, but their seeds do not exhibit the stringent dormancy of early pioneers and smaller gap sizes are required for their seeds germination) and early pioneer species (these species could not regenerate under a closed canopy but required some level of disturbance to open up gaps in the canopy), as suggested by Swaine and Whitmore (1988), and Moles and Drake (1999). Species were further classified in relation to seed size according to the following size classes: those greater than 10 mm in length being considered large, 5–10 mm in length considered medium, and less than 5 mm in length considered small (Janson 1983; Dew and Wright 1998). Thorns, spines, and prickles are three types of structures that appear in plants which have a similar appearance, but which are derived from different plant organs. We used the term ‘thorn’ in reference to all three in this paper.

Designation of species attributes was based on: (1) the field observation and our own knowledge of the flora sampled in relation to seed morphology; (2) the information from published literatures (e.g. You 1983; Lin and Cao 2009); and (3) inspection of the specimen records mainly from the Chinese Virtual Herbarium (<http://www.cvh.org.cn/>).

Data analyses

Species basal area (BA, m²) was calculated from DBH data of woody species individuals and the relative proportion of each species' basal area in percent was calculated [Relative basal area (RBA)]. The RBA of each species was then used as abundance measure of species in a community (Ohsawa 1984). The processed data was analyzed by PC-ORD version 4 (McCune and Mefford 1999) and cluster analysis was performed using distance measure of Sorensen (Bray–Curtis method).

All data were assessed by the statistics software and have normal distribution and homoscedasticity before analysis. Thus, ANOVA and *t*-test were used in our study. Mean values of variables for areas of 10 m × 10 m (mean values calculated from 4 plots of four belt transects) or each zone (mean values calculated from 12 to 28 plots of four belt transects) along the forest interior-edge-exterior gradients were analyzed with ANOVA. Difference in the abundance and basal area between thorned and unthorned lianas in each zone was tested by *t*-test. Level of significance was set at $P < 0.05$. All statistical analyses were done using the SPSS (Version 13) statistical software (SPSS Inc. Chicago, USA).

Results

Floristic composition and vegetation structure

In four 10 m × 200 m transects, 174 species were found in 136 genera and 64 families (see Table S1 in Electronic Supplementary Material). These species were distributed among 46 trees, 22 shrubs, 79 herbs, and 27 lianas, or among 38 primary species, 71 late secondary species, and 65 early pioneer species. Based on the quantitative vegetation data from eighty 100 m² quadrats of four belt transects, which were grouped into four distinct zones. Major canopy trees in zone 1 (–50 to 0 m) were evergreen broad-leaved species *L. xylocarpus*, *C. wattii*, and *L. jingdongensis*. Zone 2 (0–50 m) was dominated by *A. nepalensis* and *L. ovalifolia*. The dominant species in zone 3 (50–120 m) were *L. ovalifolia*, *R. heterophylla*, and *P. armandii*. Finally, zone 4 (120–150 m) was dominated by *L. ovalifolia*, *H. uralum*, and the herbs *E. adenophorum* (Fig. 2).

We also analyzed the life-form spectra of the four zones using percentage of species richness along the forest interior-edge-exterior gradients (Fig. 3). The proportion of trees decreased significantly across the forest-field gradients (ANOVA, $P < 0.05$). The proportion of lianas was significantly greater in zone 2 than in the other zones (ANOVA, $P < 0.05$). The proportion of herbs in zone 4 was significantly greater than in the other zones (ANOVA, $P < 0.05$). However, shrubs showed no significant variation across the edge gradients (ANOVA, $P > 0.05$). In addition, basal area of woody plants and community height decreased significantly across the forest-field gradients (ANOVA, $P < 0.05$; Fig. 4a, b). Herbaceous cover was significantly higher in zone 3 and zone 4 than in zone 1 and zone 2 (ANOVA, $P < 0.05$; Fig. 4c).

Lianas

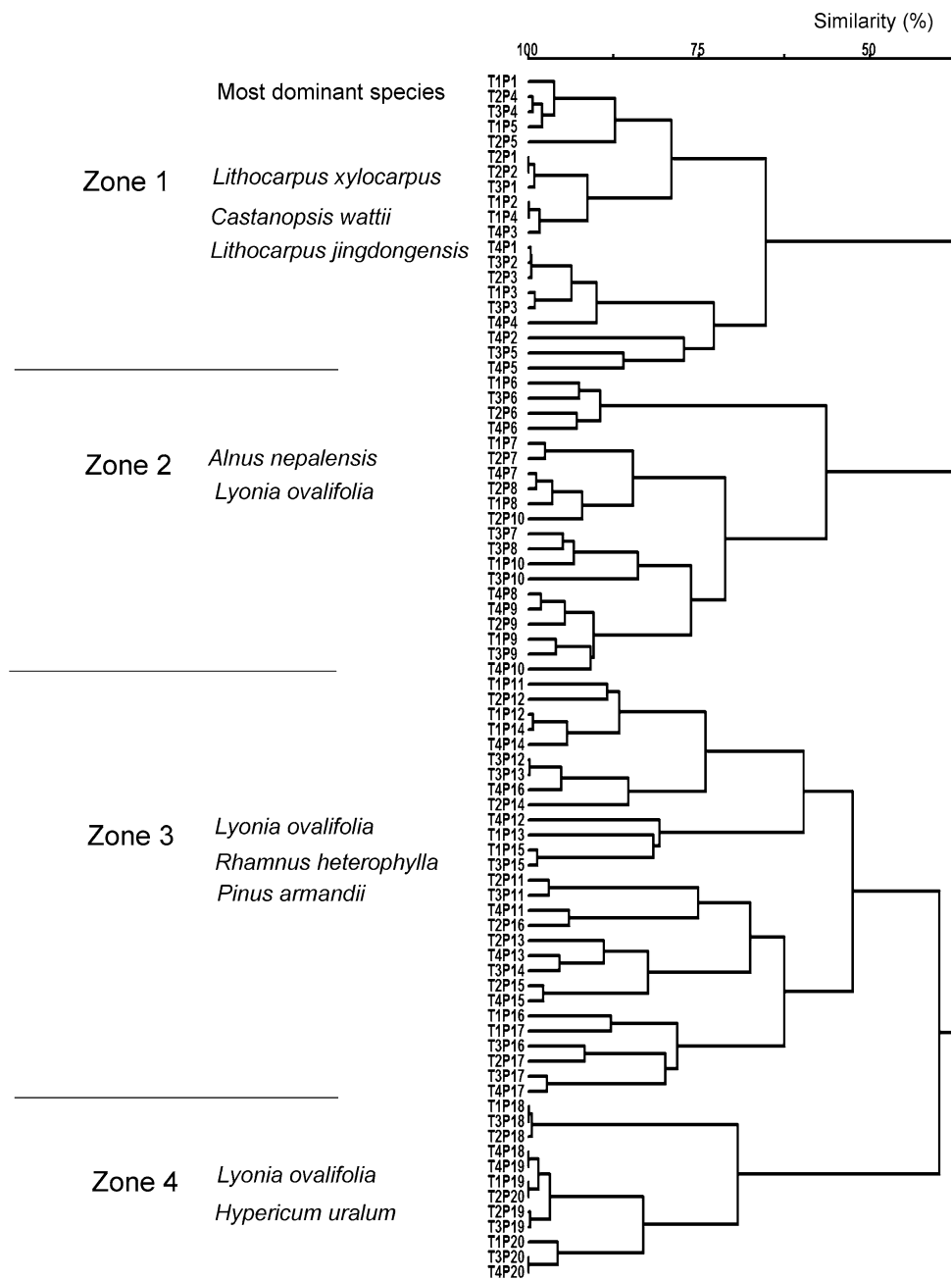
Basal area, species richness and abundance of lianas were significantly greater in zone 2 in comparison with the other zones (ANOVA, $P < 0.05$; Fig. 5a–c). The abundance and basal area of thorned lianas was significantly higher than that of unthorned lianas ($t = 20.10$, $P < 0.01$; $t = 4.46$, $P < 0.05$) in zone 2, respectively. Of the 27 liana species, the most abundant species was *Rubus corchorifolius*, followed by *Rosa longicuspis* and *Smilax lebrunii*, which were thorned lianas.

Regeneration patterns of tree species

Trees of primary species only occurred in zone 1 and zone 2, and were not found at the distances more than 50 m from the edge into the forest exterior, whereas no poles were found at the distances >70 m. The saplings and seedlings of primary species, which occurred at the distances <70 and 140 m respectively, decreased significantly in stem density across the forest-field gradients (ANOVA, $P < 0.05$; Fig. 6a). Trees of late secondary species only occurred at the distance less than 70 m. Stem density of poles and seedlings were higher in zone 2 than in the other zones, and more saplings occurred in zone 2 and zone 3 (Fig. 6b). Trees of early pioneer species only occurred at the distances 0–80 m. The seedlings were infrequent and sparse, at the same time, the poles and saplings were absent across the forest-field gradients (Fig. 6c).

Regeneration patterns of dominant canopy species of the interior forest along the forest interior-edge-exterior gradients were shown in Fig. 7. Trees of *L. xylocarpus*, *L. jingdongensis*, and *C. wattii* were only found in the forest interior (Fig. 7a–c). The poles of *L. xylocarpus* occurred at the distances <40 m. However, the poles of *L. jingdongensis*, and *C. wattii* occurred at the distances <30 and 20 m, respectively. The saplings and seedlings of the three

Fig. 2 Dendrogram showing floristic similarity between plots across the forest-field gradients



dominant canopy species were higher in zone 2 than in the other zones, and no saplings and seedlings were found at the distances >50 m from the edge into the forest exterior.

Regeneration patterns of shrub species

Primary shrub species showed a significant decrease in stem density across the forest-field gradients (ANOVA, $P < 0.05$), and were absent at the distances more than 40 m from the edge into the forest exterior (Fig. 8a). Late secondary shrub species were infrequent in the forest interior, and abundance was significantly higher in zone 2.

Moreover, there was a sharp decrease in the abundance of late secondary shrub species in zone 3 and zone 4 (Fig. 8b). The abundance of early pioneer shrub species was significantly greater at the distances more than 50 m from the edge into forest exterior, and was infrequent in zone 2, whereas it was absent in the forest interior (Fig. 8c).

Seed size and forest regeneration

The richness of primary species showed a decrease with increasing distances from the forest edge to the exterior

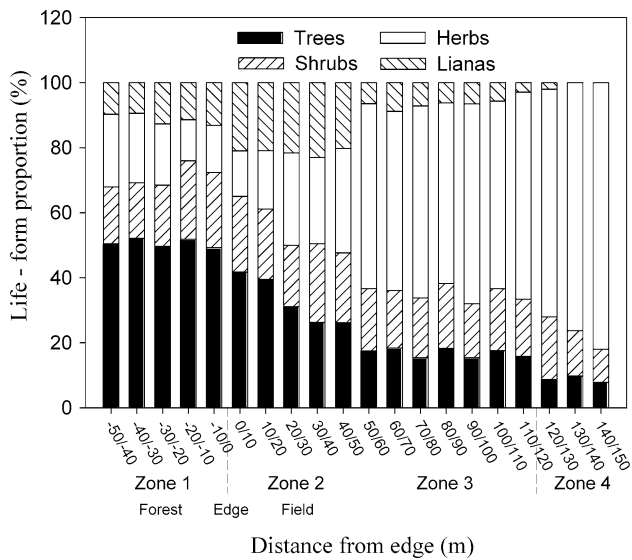


Fig. 3 Changes in life-form proportion across the forest-field gradients

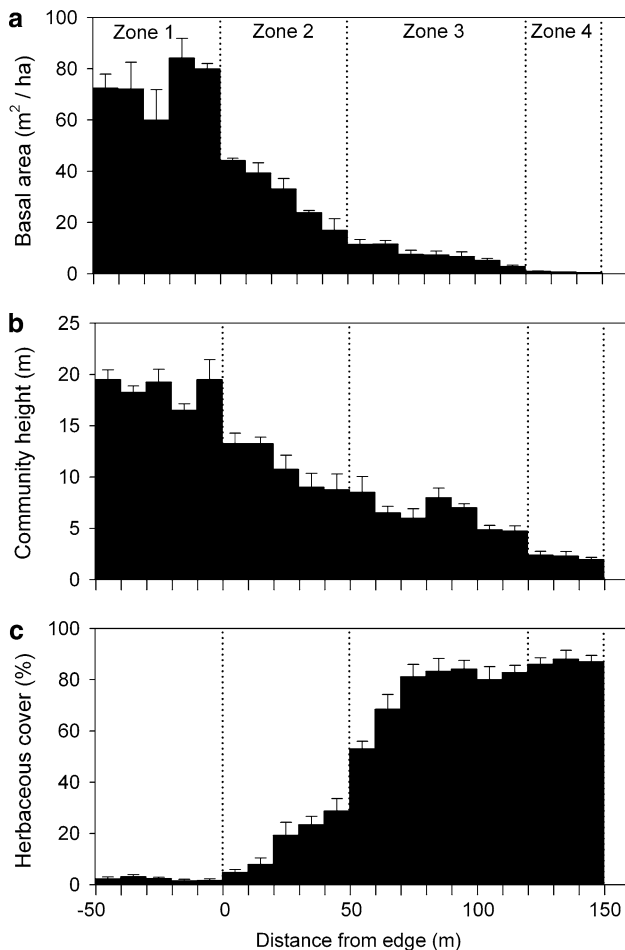


Fig. 4 Changes in basal area (a), community height (b), herb percent cover (c) across the forest-field gradients. Error bars are one standard deviation

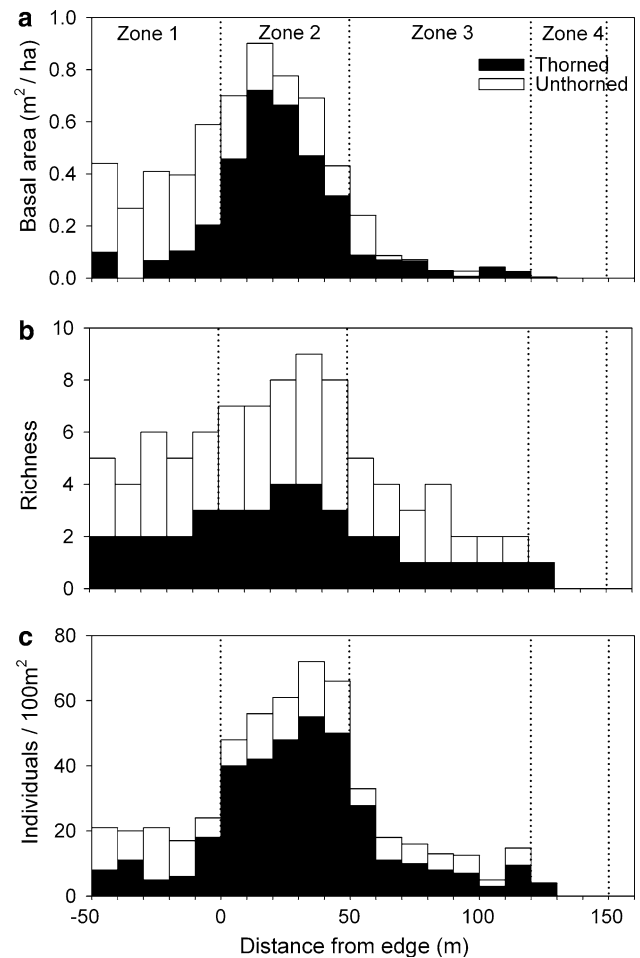


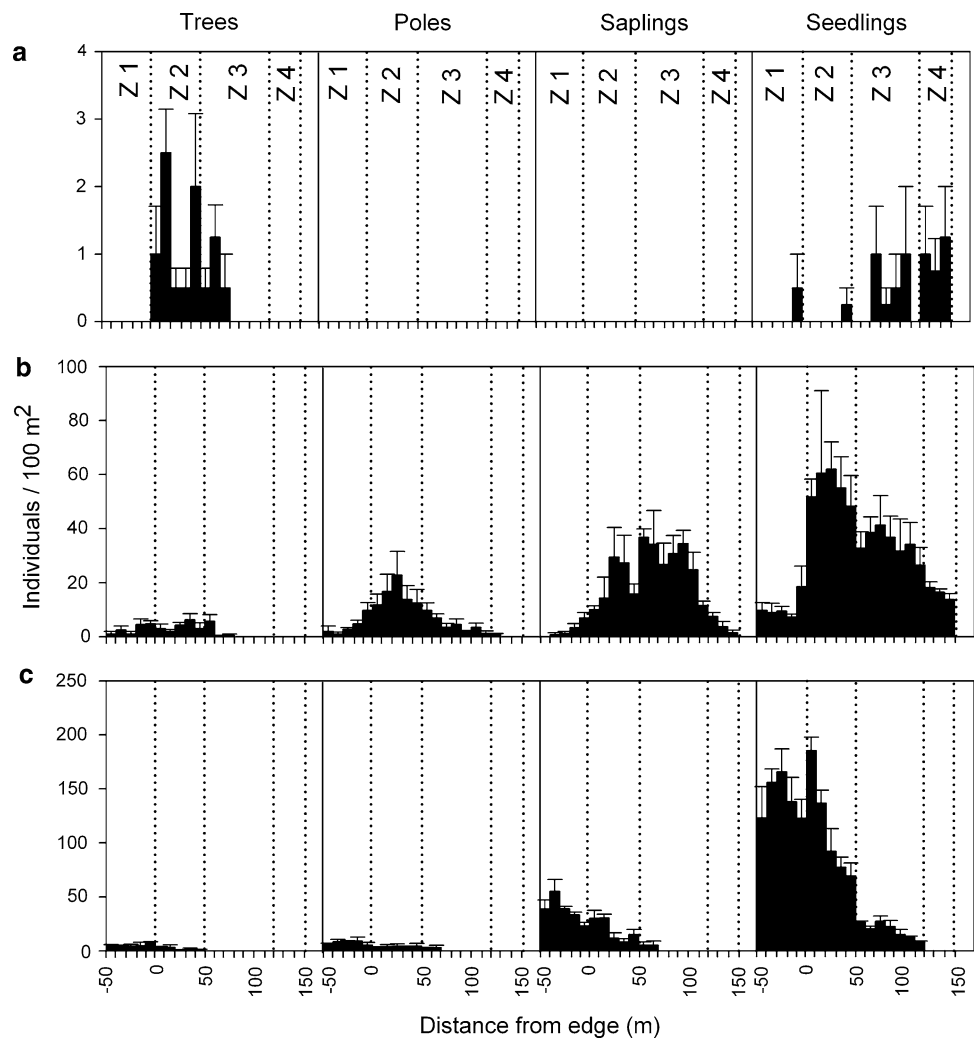
Fig. 5 Changes in basal area (a), richness (b), and stem density (c) of lianas in a $10\text{ m} \times 10\text{ m}$ plot across the forest-field gradients

(ANOVA, $P < 0.05$; Fig. 9). Number of medium-seeded primary species was greater than of small-seeded and large-seeded primary species in the interior forest and near the forest edge to the exterior (0–50 m). However, the richness of small-seeded primary species was greater than that of medium-seeded and large-seeded primary species at the distance more than 50 m from the edge into the forest exterior. Moreover, no large-seeded primary species were found at the distances >60 m from the edge into the forest exterior.

Discussion

According to the land use history of the study site, about 20 years has passed after creation of the edge. Twenty years could be sufficient to regenerate for primary species including *L. xylocarpus*, *C. wattii*, *L. jingdongensis*, *Eurya yunnanensis*, *Ilex mannei*, *I. szechwanensis*, *Lindera thomsonii*, *Litsea elongate* in the edges. Our results showed

Fig. 6 Changes in stem density of trees, poles, saplings, and seedlings for early pioneer tree species (a), late secondary tree species (b), and primary tree species (c) in a 10 m × 10 m plot across the forest-field gradients. Error bars are one standard deviation. Z1 Zone1; Z2 Zone2; Z3 Zone3; Z4 Zone4

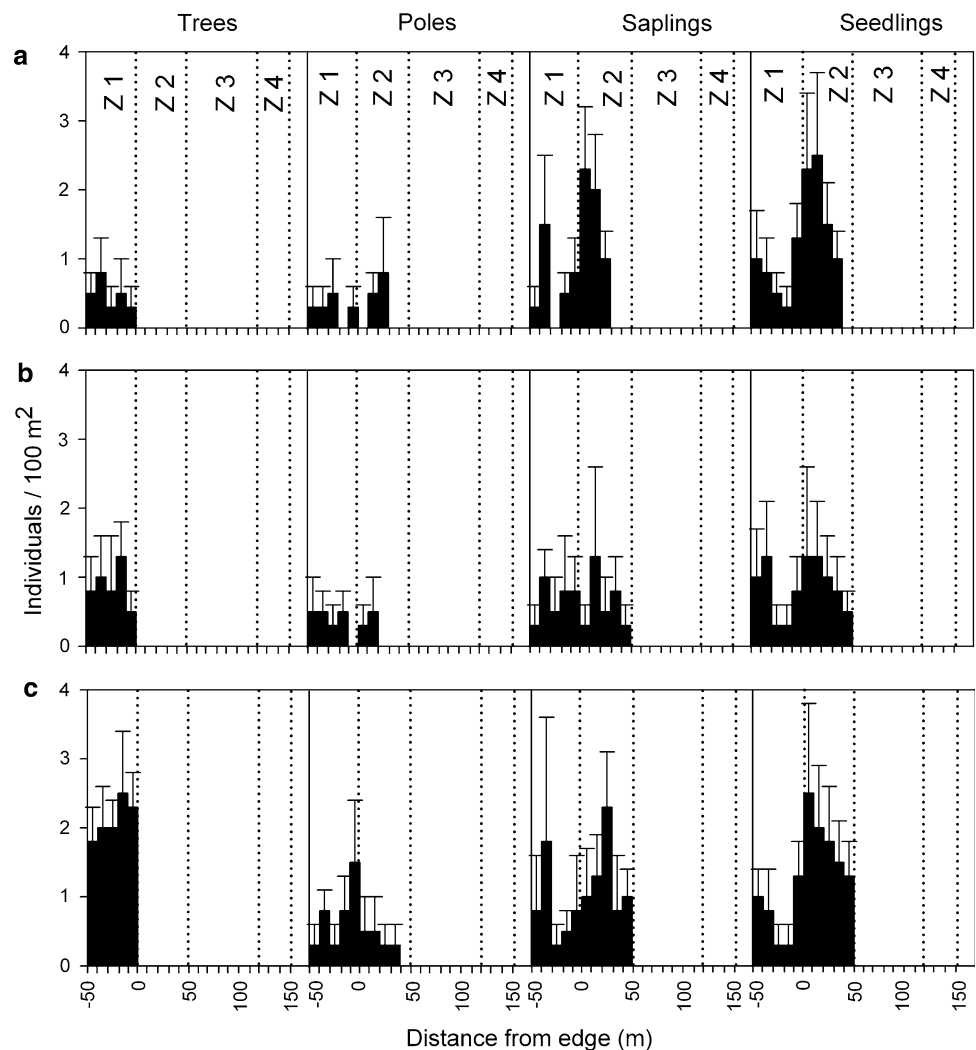


that there was a higher stem density of primary species at the distances 0–50 m than at the distances more than 50 m from the edge into the forest exterior, particularly of dominant canopy trees *L. xylocarpus*, *L. jingdongensis*, and *C. wattii* which were only confined to the distances less than 50 m. This may be because that, as previously suggested, the edge environment which passes sufficient time after creation of the edge has more favorable radiation, moisture, and temperature conditions for the establishment and survival of seedlings (Jose et al. 1996; Cadenasso and Pickett 2001). Alternatively, it has been early suggested that thorns, spines, and prickles have physical defensive protection against herbivores browsing, thereby facilitating forest regeneration (Milewski et al. 1991), though some minor damages by herbivores occurred in our study site, which are not significant through assessments by the Management Authority of the Ailao Mountain Nature Reserve. Kuiters and Slim (2003) found that the density of woody regeneration was more than 20 times in habitats

with bramble (thorny species) as compared with in habitats of open grass. As well, Sharam et al. (2009) found that the seedlings were less browsed, and consequently showed higher survival under thorny shrubs than under non-thorny shrubs. It was evident that there were more lianas near the forest edge (Fig. 5a, c), especially thorny lianas. Therefore, the dense growth of lianas and late secondary species along the edge of a forest act as a wall that may deter the large herbivores access to it (Williams-Linera 1990). Our results, combined with the previously reported results, revealed that the regeneration pattern of primary species near the montane moist evergreen broad-leaved forest edge may be closely related to the abundance of thorny lianas.

Indeed, seed predation by all seed predators is often greatest in areas of high structural complexity (Ida and Nakagoshi 1996; Manson and Stiles 1998; Caccia and Ballaré 1998). For example, Abe et al. (2001) reported that predation caused the largest proportion of *Fagus crenata* seed and seedling mortality under *Sasa* cover at both

Fig. 7 Changes in stem density of trees, poles, saplings, and seedlings for *L. xylocarpus* (a), *C. watti* (b), and *L. jingdongensis* (c) in a 10 m × 10 m plot across the forest-field gradients. Error bars are one standard deviation. Z1 Zone1; Z2 Zone2; Z3 Zone3; Z4 Zone4



canopy-closed and *Sasa*-live sites, probably because of the high density of, or active predation by, predators. Thus, it may be disadvantage for primary species regeneration under dense forest canopy and undergrowth. Similarly, abundance of seed predators (e.g., ants, beetles, rodents, birds) is commonly higher near forest edges (Restrepo et al. 1999; Duncan and Duncan 2000; Kollmann and Buschor 2002). While some studies have documented that the forest edge receives the highest amount of seeds from other habitats (Stapanian and Smith 1986; Aide and Cavelier 1994; Arrieta and Suárez 2005). Although, a large proportion of dispersed seeds are consumed by seed predators (Miyaki and Kikuzawa 1988; Herrera 1995), there are a small proportion of cached seeds for later consumption, forgotten by dispersers (Díaz 1992; Gómez et al. 2008). Smith and Reichman (2002) suggested that higher seed removal in the edge of the forest might represent higher seed dispersal as a proportion of the cached seeds might survive. In addition, small primary species seeds passing the digestive tracts undamaged in the forest edge might

also enhance regeneration (Nalepa and Piper 1994; Manson and Stiles 1998). Therefore, forest edge may be function as a “safe site” for a number of birds and annuals facilitating seed dispersal into microsites and favorable for seed germination and seedling growth (Machtans et al. 1996).

Our results differ substantially from previous studies in tropical forests, where forest regeneration is severely impeded near edges (Viana et al. 1997; Benítez-Malvido 1998; Laurance et al. 1998; Benítez-Malvido 2003; Benítez-Malvido and Martínez-Ramos 2003; Laurance et al. 2006), likely because of climatic condition differences and some distinctive ecological features of forest species. Abundant precipitation and year round warmth in the tropical forest favor the establishment and spread of pioneer species (Ferreira 1997; Laurance et al. 1998; Benítez-Malvido and Martínez-Ramos 2003). Especially, lianas could grow fast and form a dense crown, and suppress primary species growth and survival near edges (Laurance et al. 2001; Benítez-Malvido and Martínez-Ramos 2003). In addition, most tropical rain forest woody species

produce recalcitrant seeds which may be prevented germination by a hotter and drier environment near the forest edge (Benítez-Malvido 1998; Bruna 1999; Benítez-Malvido and Martínez-Ramos 2003). Correspondingly, in subtropical mountains, woody vegetation grows slowly under high altitude and relatively high humidity (Liu et al. 2002; Vreeland and Tietje 2004). Specifically, the evergreen broad-leaved forest has more dormant than non-dormant seeds in relation to the tropical rainforest (Baskin and Baskin 2008). Dormant seeds may overcome or escape unfavorable conditions for seedling survival and growth (Teketay 2005).

The stem density of primary species had a sharp decrease at the distances more than 50 m from the edge into the forest exterior; moreover, no individuals of the three dominant canopy species were found at the distances >50 m. The same pattern of a sharp decline in the abundance of woody primary species with distance from edge has also been observed in a Costa Rican upper montane cloud forest (Oosterhoorn and Kappelle 2000), and in European and North American deciduous forests in which *Quercus* and *Carpinus* are important canopy components (Myster and Pickett 1992; Lawson et al. 1999). Presumably, there may be following causes for this pattern:

Firstly, lack of seed dispersal is a major limiting factor in natural forest regeneration. Because most animals, especially large mammalian frugivores infrequently enter far into abandoned pastures, and thus animal dispersal of seeds very rarely occurred at sites far from the forest edge (Aide and Cavelier 1994; Cardoso da Silva et al. 1996; Chapman and Chapman 1999). Studies in other areas of Central and South America have confirmed that seed dispersal was a major factor limiting natural regeneration following pasture abandonment (Aide and Cavelier 1994; Zimmermann et al. 1994). Evidently, the abundance of primary woody species showed a decrease with increasing a distance from the edge into the forest exterior (Fig. 6c and Fig. 8c); and our results also provided evidence that the medium-seeded primary species showed a drastic decrease with an increasing distance, and the large-seeded primary species did not occur at the distances more than 60 m (Fig. 9).

Again, the harsh physical conditions of open areas may present higher light availabilities (Jose et al. 1996), higher air and soil temperature (Williams-Linera et al. 1998; Didham and Lawton 1999), lower soil and litter moisture (Jose et al. 1996), and lower relative humidity (Didham and Lawton 1999), which preclude many primary species from regenerating (Nepstad et al. 1996).

Further, we found a high density of herbaceous plants (e.g. *E. adenophorum*) and early pioneer shrub species (e.g. *Osbeckia opipara*, *Gaultheria forrestii*, *H. uralum*) at the distance more than 50 m (Fig. 4c and Fig. 8a). Even in

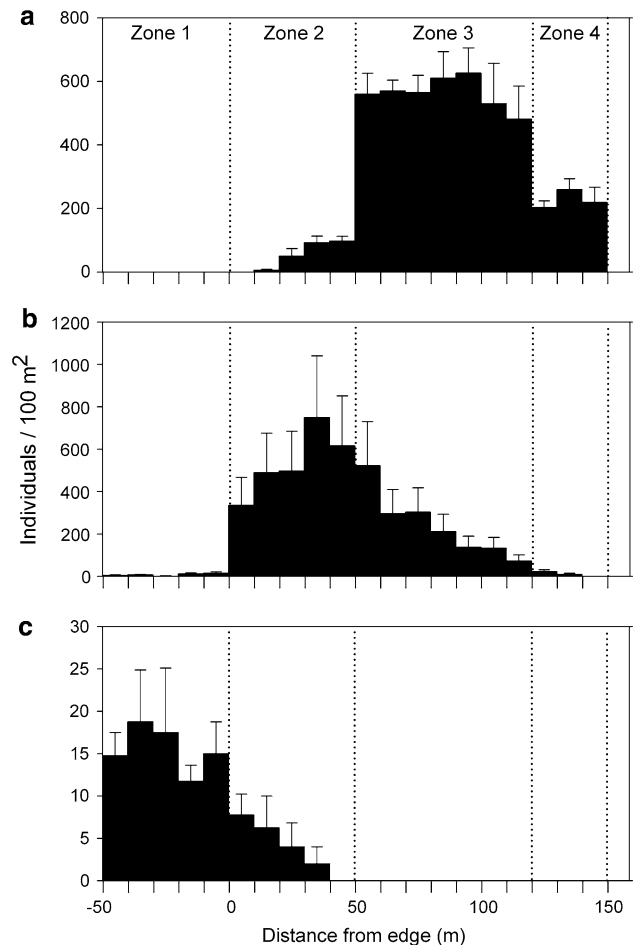


Fig. 8 Changes in stem density of early pioneer shrub species (a), late secondary shrub species (b), and primary shrub species (c) in a 10 m × 10 m plot across the forest-field gradients. Error bars are one standard deviation

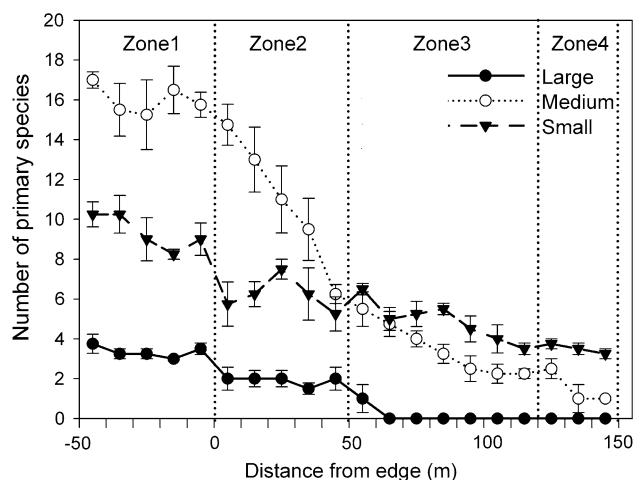


Fig. 9 Changes in number of large-seeded, medium-seeded, and small-seeded primary species in a 10 m × 10 m plot across the forest-field gradients. Error bars are one standard deviation

sites where the seeds of primary species are able to germinate, competitions with early pioneer shrub and herb species for limited nutrients and water may limit the growth and survivorship of seedlings (Gerhardt 1993). In addition, animals grazing and trampling may be factors preventing, or restricting the regeneration of primary species (Coomes et al. 2003).

In conclusion, after 20 years of the edge creation, we found that there were more individuals of primary species at the distances 0–50 m compared with the distances more than 50 m from the edge into the forest exterior. The dominant canopy trees *L. xylocarpus*, *C. wattii*, and *L. jingdongensis* of the interior forest were only confined to the distances less than 50 m. A reasonable interpretation might be that the higher abundance of thorny lianas and late secondary species in the edge of a forest not only act as a “wall” which may hinder the large herbivores access to it, but also function as “safe habitat” for small mammals facilitating seed dispersal into microsites. However, a dense early pioneer shrub and exotic species *E. adenophorum* in the outside of forest and seed dispersal might be the major factors limiting the primary species regeneration. Thus, these results bring important information that once this forest has been destroyed, managers should be aware of crucial importance to protection the forest edge which as a buffer zone may induce forest recovery processes, and should give priority to the protection of this forest edge.

Acknowledgments This work was supported by Natural Science Foundation of China (No. 30771705), the Knowledge Innovation Program (No. KSCX2-YW-N066-03), and the Program of Hundreds of Talent Scientists of the Chinese Academy of Sciences (BRJH2002098). The Management Authority of the Ailao Mountain Nature Reserve is thanked for granting permission to undertake the research reported. Li Dawen, Yang Wenzheng, Qi Jinhua, and other staff members of the Ailao Mountain Forest Ecosystem Research Station are thanked for their help in the field work. We also thank Prof. Min Cao and Dr. Luxiang Lin whose valuable comments helped us to improve the paper greatly.

References

- Abe M, Miguchi H, Nakashizuka T (2001) An interactive effect of simultaneous death of dwarf bamboo, canopy gap, and predatory rodents on beech regeneration. *Oecologia* 127:281–286
- Aide TM, Cavelier J (1994) Barriers to tropical lowland forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restor Ecol* 2:219–229
- Arrieta S, Suárez F (2005) Spatial dynamics of *Ilex aquifolium* populations seed dispersal and seed bank: understanding the first steps of regeneration. *Plant Ecol* 177:237–248
- Bakker ES, Olf H, Vandenberghe C, De Maeyer K, Smit R, Gleichman JM, Vera FWM (2004) Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *J Appl Ecol* 41:571–582
- Baskin CC, Baskin JM (2008) Advances in understanding seed dormancy at the whole-seed level: an ecological, biogeographical and phylogenetic perspective. *Acta Bot Yunnanica* 30:279–294
- Benítez-Malvido J (1998) Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conserv Biol* 12:380–389
- Benítez-Malvido J (2003) Influence of edge exposure on tree seedling species recruitment in tropical rain forest fragments. *Biotropica* 35:530–541
- Benítez-Malvido J, Martínez-Ramos M (2003) Impact of forest fragmentation on understory plant species richness in Amazonia. *Conserv Biol* 17:389–400
- Bruna EM (1999) Seed germination in rainforest fragments. *Nature* 40:139
- Caccia FD, Ballaré CL (1998) Effects of tree cover, understory vegetation, and litter on regeneration of Douglas-fir (*Pseudotsuga menziesii*) in southwestern Argentina. *Can J For Res* 28:683–692
- Cadenasso ML, Pickett STA (2001) Effect of edge structure on the flux of species into forest interiors. *Conserv Biol* 15:91–97
- Cardosa da Silva JM, Uhl C, Murray G (1996) Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conserv Biol* 10:491–503
- Cavallin N, Vasseur L (2008) Potential for red spruce (*Picea rubens* Sarg.) establishment from natural seed dispersal in old fields adjacent to forest stands. *Plant Ecol* 199:33–41
- Chapman CA, Chapman LJ (1999) Forest restoration in abandoned agricultural land: a case study from east Africa. *Conserv Biol* 13:1301–1311
- Coomes DA, Allen RB, Forsyth DM, Lee WG (2003) Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conserv Biol* 17:450–459
- Coops H (1988) Occurrence of Blackthorn (*Prunus spinosa* L) in the area of Molsbjerg and the effect of cattle and sheep grazing on its growth. *Nat Jutl* 15:169–176
- Dew JL, Wright P (1998) Frugivory and seed dispersal by four species of primates in Madagascar’s eastern rain forest. *Biotropica* 30:425–437
- Díaz M (1992) Rodent seed predation in cereal crop areas of central Spain: effects of physiognomy, food availability and predation risk. *Ecography* 15:77–85
- Dickerman MB, Duncan DP, Gallegos CM, Clark FB (1981) Forestry today in China: report of a month’s tour by a team of American foresters. *J For* 79:71–75
- Didham RK, Lawton JH (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31:17–30
- Duncan RS, Duncan VE (2000) Forest succession and distance from forest edge in an Afro-Tropical Grassland. *Biotropica* 32:33–41
- Euskirchen ES, Chen J, Bi R (2001) Effects of edges on plant communities in a managed landscape in northern Wisconsin. *For Ecol Manage* 148:93–108
- Ferreira LV (1997) Effects of the duration of flooding on species richness and floristic composition in three hectares in the Jaú National Park in floodplain forests in central Amazonia. *Biodivers Conserv* 6:1353–1363
- Ferreira LV, Laurance WF (1997) Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. *Conserv Biol* 11:797–801
- Fraver S (1994) Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke river basin, North Carolina. *Conserv Biol* 8:822–832
- Gehlhausen SM, Schwartz MW, Augspurger CK (2000) Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecol* 147:21–35

- Gerhardt K (1993) Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. *J Veg Sci* 4:95–102
- Godínez-Álvarez H, Valiente-Banuet A, Rojas-Martínez A (2002) The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*. *Ecology* 83:2617–2629
- Gómez JM, Puerta-Piñero C, Schupp EW (2008) Effectiveness of rodents as local seed dispersers of Holm oaks. *Oecologia* 155:529–537
- Herrera J (1995) Acorn predation and seedling production in a low-density population of cork oak (*Quercus suber* L.). *For Ecol Manage* 76:197–201
- Hill MO, Wallace HL (1989) Vegetation and environment in afforested sand dunes at Newborough, Anglesey. *Forestry* 62:249–267
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:201–228
- Ida H, Nakagoshi N (1996) Gnawing damage by rodents to the seedlings of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* in a temperate *Sasa* grassland-deciduous forest series in southern Japan. *Ecol Res* 11:97–103
- Janson CH (1983) Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219:187–189
- Jose S, Andrew RG, George SJ, Kumar BM (1996) Vegetation responses along edge-to-interior gradients in a high altitude tropical forest in peninsular India. *For Ecol Manage* 87:51–62
- Kira T (1991) Forest ecosystems of east and southeast Asia in global perspective. *Ecol Res* 6:185–200
- Kollmann J, Buschor M (2002) Edges effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecol* 164:249–261
- Kuiters AT, Slim PA (2003) Tree colonisation of abandoned arable land after 27 years of horse-grazing: the role of bramble as a facilitator of oak wood regeneration. *For Ecol Manage* 181:239–251
- Laurance WF (1991) Edge effects in tropical forest fragments: application of a model for the design of nature reserves. *Biol Conserv* 57:205–219
- Laurance WF (1997) Hyper-disturbed parks: edge effects and the ecology of isolated rainforest reserves in tropical Australia. In: Laurance WF, Bierregaard RO (eds) *Tropical forest remnants: ecology, management and conservation of fragmented communities*. University of Chicago Press, Chicago, pp 71–83
- Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG (1998) Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79:2032–2040
- Laurance WF, Perez-Saliciprup D, Delamonica P, Fearnside PM, D'Angelo S, Jerozolinski A, Pohl L, Lovejoy TE (2001) Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82:105–116
- Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, Capretz RL (2006) Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87:469–482
- Lawson D, Inouye RS, Huntly N, Carlson WP (1999) Patterns of woody plant abundance, recruitment, mortality, and growth in a 65 year chronosequence of old-fields. *Plant Ecol* 145:267–279
- Lin L, Cao M (2009) Edge effects on soil seed banks and understory vegetation in subtropical and tropical forests in Yunnan, SW China. *For Ecol Manage* 257:1344–1352
- Liu WY, Fox JED, Xu ZF (2002) Litterfall and nutrient dynamics in a montane moist evergreen broad-leaved forest in Ailao Mountains, SW China. *Plant Ecol* 164:157–170
- López-Barrera F (2003) Edge effects in a forest mosaic: implications for oak regeneration in the Highlands of Chiapas, Mexico. Ph.D. Thesis. Institute of Atmospheric and Environmental Science, University of Edinburgh, Edinburgh, UK
- Machtans CS, Villard MA, Hannon SJ (1996) Use of riparian buffer strips as movement corridors by forest birds. *Conserv Biol* 10:1366–1379
- Manson RH, STILES EW (1998) Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos* 82:37–50
- McCune B, Mefford MJ (1999) PC-ORD: multivariate analysis of ecological data, Version 4. MjM Software Design, Gleneden Beach
- Milewski AV, Young TP, Madden D (1991) Thorns as induced defenses: experimental. *Oecologia* 86:70–75
- Miyaki M, Kikuzawa K (1988) Dispersal of *Quercus mongolica* acorns in a broadleaved deciduous forest. 2. Scatterhoarding by mice. *For Ecol Manage* 25:9–16
- Moles AT, Drake DR (1999) Potential contributions of the seed rain and seed bank to regeneration of native forest under plantation pine in New Zealand. *New Zeal J Bot* 37:83–93
- Mwima PM, McNeilage A (2003) Natural regeneration and ecological recovery in Bwindi Impenetrable National Park, Uganda. *Afr J Ecol* 41:93–98
- Myster RW, Pickett STA (1992) Effects of palatability and dispersal mode on spatial patterns of trees in old-fields. *Bull Torrey Bot Club* 119:145–151
- Nalepa CA, Piper WH (1994) Bird dispersal of the larval stage of a seed predator. *Oecologia* 100:200–202
- Nepstad D, Uhl C, da Silva JMC (1996) A comparative study of tree establishment in abandoned pasture and mature forest in eastern Amazonia. *Oikos* 76:25–39
- Ohsawa M (1984) Differentiation of vegetation zones and species strategies in the subalpine region of Mt. Fuji. *Vegetatio* 57:15–52
- Oloff H, Vera FWM, Bokdam J, Bakker ES, Gleichman JM, de Maeyer K, Smit R (1999) Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biol* 1:27–137
- Oosterhoorn M, Kappelle M (2000) Vegetation structure and composition along an interior-edge-exterior gradient in a Costa Rican montane cloud forest. *For Ecol Manage* 126:291–307
- Pandey SK, Shukla RP (2003) Plant diversity in managed sal (*Shorea robusta* Gaertn.) forests of Gorakhpur, India: species composition, regeneration and conservation. *Biodivers Conserv* 12:2295–2319
- Restrepo C, Gómez N, Heredia S (1999) Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a neotropical montane forest. *Ecology* 80:668–685
- Sharam GJ, Sinclair ARE, Turkington R, Jacob AL (2009) The savanna tree *Acacia polyacantha* facilitates the establishment of riparian forests in Serengeti National Park, Tanzania. *J Trop Ecol* 25:31–40
- Smith CC, Reichman OJ (2002) The evolution of food caching by birds and mammals. *Annu Rev Ecol Syst* 15:329–351
- Stapanian MA, Smith CC (1986) How fox squirrels influence the invasion of prairies by nut-bearing trees. *J Mammal* 67:326–332
- Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86
- Tagawa H (1995) Distribution of lucidophyll oak-laurel forest formation in Asia and other areas. *Tropics* 5:1–40
- Tanouchi H, Yamamoto S (1995) Structure and regeneration of canopy species in an old-growth evergreen broad-leaved forest in Aya district, southwestern Japan. *Vegetatio* 117:51–60
- Tashi S (2004) Regeneration of *Quercus semecarpifolia* Sm. in an old growth oak forest under Gidakom FMU- Bhutan. M. Sc. Thesis. Wageningen University and Research Centrum, Wageningen

- Teketay D (2005) Seed and regeneration ecology in dry Afromontane forests of Ethiopia. I. Seed production–population structures. *Trop Ecol* 46:29–44
- Viana VM, Tabanez AAJ, Batista JLF (1997) Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. In: Laurance WF, Bierregaard RO Jr (eds) *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. The University of Chicago Press, Chicago, pp 351–365
- Vreeland JK, Tietje WD (2004) Vegetative structure of woodland-grassland edges in coastal central California. *Southwest Nat* 49:305–310
- Wang XH, Kent M, Fang XF (2007) Evergreen broad-leaved forest in Eastern China: its ecology and conservation and the importance of resprouting in forest restoration. *For Ecol Manage* 245:76–87
- Williams-Linera G (1990) Vegetation structure and environmental conditions of forest edges in Panama. *J Ecol* 78:356–373
- Williams-Linera G, Dominguez-Gastelu V, Garcia-Zurita ME (1998) Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conserv Biol* 12:1091–1102
- You CX (1983) Classification of vegetation in Xujiaba region in Ailao Mts. In: Wu ZY (ed) *Research of forest ecosystems of Ailao Mountains, Yunnan* (in Chinese with English abstract). Yunnan Science and Technology Press, Kunming, pp 74–117
- Zhu WZ, Cheng S, Cai XH, He F, Wang JX (2009) Changes in plant species diversity along a chronosequence of vegetation restoration in the humid evergreen broad-leaved forest in the Rainy Zone of West China. *Ecol Res* 24:315–325
- Zimmerman JK, Everham EM III, Waide RB, Lodge DJ, Taylor CM, Brokaw NVL (1994) Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical life histories. *J Ecol* 82:91–922