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RESEARCH ARTICLE

Use of Fruit Essential Oils to Assist Forest Regeneration by Bats

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Abstract

Frugivorous bats can be attracted with essential oils from ripe chiropterochoric fruit. We evaluated the efficiency of these oils to attract bats in degraded areas within the Atlantic Rain Forest, particularly pasture and agricultural land. We hypothesized that induction units (IUs), each containing a rubber septum impregnated with oil, would have more bat activity than their respective control units (CUs; without the oil). To test this hypothesis we monitored bat flight activity with night-vision infrared visors in eight IU and CU from August 2006 to July 2007. We also verified the probability of arrival of chiropterochoric seeds by analyzing the diet of bats captured in a neighboring forest area. Our initial hypothesis that units with odor would lead to greater bat activity was confirmed. Results indicated a rich community of fruit-eating bats, and dietary analysis revealed a huge potential for dispersion of a vast amount of seeds from different plant species at the IU. Although our study does not reveal with certainty which bat species are attracted to the oil, the flying patterns coincide with those described for the foraging behavior of fruit-eating phyllostomids. Furthermore, the fact that the bats spend more time flying around the odor source compared to flying time around CU suggest an increase in seed rain. Taken together, these results suggest that the use of essential oils from chiropterochoric fruits induces a qualitative and quantitative increase in seed dispersal in areas that otherwise would not be frequently visited by frugivorous bats.

Key words: **Atlantic Forest, bat attraction, conservation biology, frugivory, fruit-eating bats, fruit odors, restoration, seed dispersal.**

Introduction

The Brazilian Atlantic Rain Forest is one of the most diverse and threatened biomes in the world (Mittermeier et al. 2005). Remaining areas of Atlantic Forest suffer intense pressures from a variety of anthropogenic activities carried out by a population of more than 120 million people (Fundação SOS Mata Atlântica/INPE 2008) in the surrounding areas. Today, more than 92% (about 1,200,000 km^2) of the original continuous forest landscape (Campanili & Prochnow 2006) is represented by small forest remnants surrounded by an extensive agricultural matrix.

The high level of habitat loss and fragmentation of this biome has consequences that extend beyond the loss of biodiversity. The loss of forest areas also impairs other biologically and socially relevant aspects such as soil quality, the availability and quality of water, and even the use of inappropriate areas for agriculture and/or areas otherwise protected by law (e.g. Braga et al. 2002; Young & Lustosa 2003). These concerns have prompted several researchers to seek strategies to restore the original landscape and to maintain a minimal level of ecological processes to assure the continued functioning of the fragmented landscape (e.g. Bianconi et al. 2007; Tres et al. 2007; Viani et al. 2007; Kelm et al. 2008).

The success of any restoration process depends, to a large extent, on the recruitment of new individuals and plant species from the seed bank and, perhaps more importantly, the seed rain from dispersers (Jordano 2000; Gandolfi et al. 2007). In fact, seed dispersal forms the foundation for the regeneration of degraded areas, so that processes that negatively affect the mechanisms of seed dispersal limit the success of the restoration process (Aide & Cavelier 1994; Uhl 1997; Galindo-González et al. 2000). For example, when the input of seeds is too small, any single factor (i.e. predation rate, competition with the already established vegetation, adverse climate, and soil types) can compromise the germination of seeds or seedling establishment (Uhl 1997; Gandolfi et al. 2007). Thus, the process of restoration will benefit from any mechanism that maximizes seed dispersal into degraded areas.

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Vertebrates are important seed dispersal agents, having a marked effect on the functional and structural characteristics of their communities, even in restored areas (Gandolfi et al. 2007). It has been estimated that between 50 and 90% of the trees and nearly all shrub species in tropical forests possess zoochoric fruits (Howe & Westley 1988). Although several vertebrate groups can act as seed dispersers (Jordano 2000), fruit-eating bats stand out as one of the most important vectors in this context, especially in fragmented areas (Estrada & Coates-Estrada 2002; Bianconi et al. 2004; Medina et al. 2007). For example, some fruit-eating bats of the New World family Phyllostomidae commute long distances between their diurnal roosts and feeding sites and, because they defecate while flying, they can have an overwhelming influence on the spatial distribution of seeds (Fleming 1988). Thus, these behavioral characteristics make these bats pivotal elements for the restoration of otherwise degraded and/or abandoned areas.

Phyllostomid bats use olfaction to detect mature fruits (e.g. Mikich et al. 2003; Korine & Kalko 2005; Bianconi et al. 2007). Using experiments with essential oils from chiropterocoric fruits Mikich et al. (2003) and Bianconi et al. (2007) corroborated this for *Carollia perspicillata* (Seba's short-tailed bat) and *Artibeus lituratus* (Great fruit-eating bat), which are common and well-known dispersers of pioneering plants in the Neotropics (Fleming 1988). Mikich et al. (2003) showed that it was possible to attract and capture individuals of *C. perspicillata* inside forest fragments when mist nets were impregnated with essential oils of the preferred fruit consumed by this species (Piperaceae). Bianconi et al. (2007) extended these results by showing differences in the efficacy of essential oils from different fruit species (*Piper*— Piperaceae, *Solanum*—Solanaceae, and *Ficus*— Moraceae) to attract and capture fruit-eating bats in resource-scarce degraded areas situated at different distances from forest remnants.

On the basis of these results, Bianconi et al. (2007) proposed a new tool for the restoration of degraded areas, whereby fruit-eating bats would be attracted to these areas by fruit essential oils, thereby increasing seed rain and, thus, speeding up the successional processes. The idea was based on the assumption that, once these bats were attracted by olfactory cues from the essential oils to a "new food source," they would spend a certain amount of time flying around these new food sources. Given that, as hitherto stated, some of these bats commute long distances, defecate while flying, and have a fast transit time through their gastrointestinal tract (Fleming 1988), there would be a high probability of increasing seed rain in these degraded areas.

In this article, we further explore the applicability of this new tool, by testing the efficacy of essential oils from ripe chiropterochoric fruits to attract fruit-eating bats to open areas, with the use of artificial induction units (IUs) installed in a number of different locations in pasture and agricultural fields (corn, soybean) surrounding an area of Atlantic Forest in southern Brazil. Monitoring and quantifying the movements of bats around units with and without the essential oils, we tested the hypothesis that areas with IUs impregnated with the fruit odor would have larger bat activity for a longer period of time when compared to the control units (CUs). The potential for the input of seeds from chiropterochoric fruits to these areas was inferred by analyzing the diets of fruit-eating bats captured in a nearby forest fragment.

Methods

Study Area

We conducted this study in Parque Estadual Vila Rica do Espírito Santo (PVR) (23°55′S–51°57′W) and at surrounding abandoned areas of pasture and agricultural fields (23°56′S–51°56′W), in the city of Fênix, Paraná, Southern Brazil, between August 2006 and July 2007. The average elevation in the area is 330 m and the climate is Cfa or mesothermal humid subtropical (Koeppen classification), with average temperatures ranging between 16 and 29°C and yearly precipitation between 1,400 and 1,500 mm. Most precipitation occurs between December and March, without a defined dry season (Mikich & Oliveira 2003).

The remaining vegetation is part of the Atlantic Forest (*sensu lato*), in the semideciduous seasonal forest ecosystem (Veloso et al. 1992). It consists of fragments of different sizes (<600 ha), shapes, and disturbance histories, surrounded by a matrix of agricultural fields (corn, soy, and sugar cane), some pastures, and degraded riverside vegetation. PVR has 354 ha of secondary forest, bordered by pasture and the Ivaí and Corumbataí rivers. Because of its development time (it used to be an urban and agricultural area occupied by Indians and Spaniards until 1632, when it was abandoned), vegetation is very similar to that found in primary forests of the region. For a more detailed description, including a list of species, phenology, and occupation history, see Mikich & Silva (2001) and Mikich & Oliveira (2003).

Plant Species and Isolation of Essential Oils

Essential oils were isolated from the ripe fruit of *Piper gaudichaudianum* (Kunth) (Piperaceae), collected at PVR. The fruits of the genus *Piper* are typically chiropterochoric, with a strong odor and discreet coloring, and are exposed beyond the leaves (van der Pijl 1957; Yuncker 1972). Additionally the fruits from some species ripen at dusk (Thies & Kalko 2004; Bianconi et al. 2007). In the remaining forests of the region, this genus is represented by nine species distributed along roads, trails and forest clearings, and interiors (Mikich & Silva 2001). According to Mikich & Silva (2001) *P. gaudichaudianum* is one of the most common species in the studied area. *Piper gaudichaudianum* has a fruiting peak from November to February, followed by a secondary peak from May to July. This species was selected because of its frequent consumption by frugivorous bats in the region (cf. Mikich 2002; Bianconi et al. 2006). It was also selected because of the amount of chemical (Teixeira 2003) and ecological data available, with previous experiments demonstrating that essential oils from this genera attract frugivorous bats (Mikich et al. 2003; Bianconi et al. 2007).

The isolation of essential oils was carried out using the hydro distillation technique, with a Clevenger device modified according to the German pharmacopoeia (Deutsches Arzneibuch 10, 1991), processing 300 g of fruit for 4 hours. The product of each extraction was stored in an ampoule and frozen until used. The entire procedure was performed by chemists at Embrapa Florestas.

Experimental Protocol

Each IU consisted of a "smell unit," with a natural rubber septum (Aldrich® Z100714—7 mm) impregnated with essential oils from ripe chiropterochoric fruits diluted in ether (approximately 17.5 mg/mL). The "smell unit" was suspended at the tip of a bamboo stick (circa 1.8 m high). Our experimental protocol consisted of the installation of eight of these units paired with controls (CU—without essential oils), in sampling units (20 × 20 m), located in selected sites of the agricultural (soy and corn) and pasture matrices. The distances between these units varied from 310 to 2,410 m, and the distances between them and the PVR varied from 470 to 2,340 m.

We carried out direct observations of bat overflight frequency around each unit (IU + CU) with an infrared binocular (ATN Night Scout) and digital infrared video-camera (Sony DCR-HC28). These observation sessions were carried out on a monthly basis, during four nights, by a single person (G.V.B.), usually over consecutive days during the last quarter (waning) moon phase, between the third and sixth hours after sunset (which corresponds to a period when fruit-eating bats are known to be more active—Reis 1984; Pedro & Taddei 2002; Aguiar & Marinho-Filho 2004). Each unit (IU or CU) was monitored discontinuously every month for 20 minutes and the order of observation was changed in the following month. Whenever possible, the frequency of overflight and foraging behavior (flight type, direction, time) were documented (cf. Thies et al. 1998; Korine & Kalko 2005). Even though a septum potentially can release the oil for several days, we changed the septa of all IU at the beginning of the observation session in order to equalize the amount of oil in each of them.

Bat Capture and Diet Analysis

We quantified the diet of fruit-eating bats in the study area by analyzing feces collected from bats mist-netted in the forest area (PVR). We used 10 mist-nets (12 × 2.5 m) placed in trails inside the PVR, which were opened for 6 hours after sunset. Mist-netting was carried out twice a month, so that our capture effort consisted of 43,200 m^2.h, calculated after Straube & Bianconi (2002).

After capture, bats were kept in cotton bags for a minimum of 4 hours to maximize the number of fecal samples collected. These samples were then analyzed, and their seed contents identified to the lowest possible taxonomic level by comparison with a reference collection available for the area.

Data Analysis

Differences in bat overflight frequency in the units (IU vs. CU) were analyzed by a Wilcoxon paired test (Zar 1999). Preliminary analysis showed that there was no influence of month and unit location on the frequency of bat overflight, so data were pooled for this analysis. Analysis was carried out with the Statistica software (α significance of 0.05 in all tests).

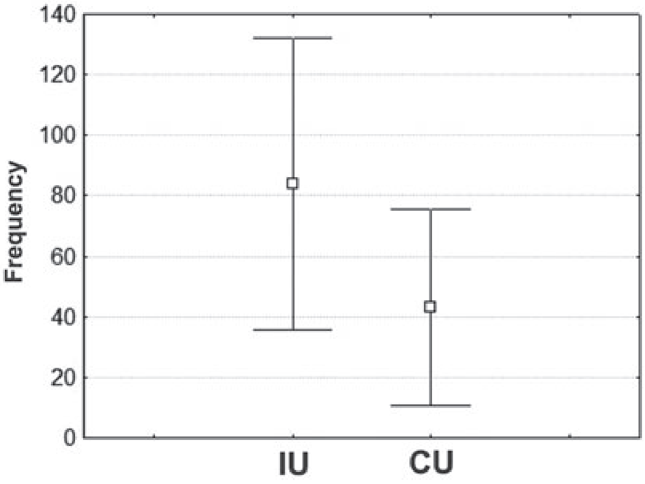

Figure 1. Mean cumulative frequency (±1 SD) of bat overflight in the experimental units (IU, induction unit; CU, control unit), between August 2006 and July 2007.

Results

Bat Overflight Around the Experimental Units

A total of 7,680 minutes of observations (320 minutes per month for each individual unit) allowed us to record a high number of overflights around the experimental units as well as to document some specific foraging behaviors toward the septa containing essential oils. The total number of observed overflights was 1,522 (Fig. 1), with the accumulated value for the IU ($n = 1{,}005$) being significantly higher ($Z = 3.06$, $p = 0.002$) than the cumulative number observed for the CU ($n = 517$).

On several occasions, we were able to record positive reactions of bats toward the IU. For example, during exploratory flights (from 1 to 4 m above ground; $n = 64$), some individuals flew in concentric circles around the parcel, reducing the flight radius toward the septum. The mean time of this exploratory behavior ranged from 1 to 4 minutes per individual (mean ± 1 SD = 1.5 ± 0.9). In other cases ($n = 147$), we recorded a straight and fast flight (at 3–5 m above ground), which always ended in an abrupt movement toward the septum. Similar behaviors were never observed around the CU, where flights were limited to rapid movements (<3 seconds), sometimes toward the IU.

Bats Captured and Diet Analysis

We captured 273 individuals of nine species, all belonging to Phyllostomidae, in the forest area. Seven out of these nine

Table 1. Number, relative abundance, and diet of bat species captured in the forest area between August 2006 and July 2007.

Species	*Diet*	*Number of Individuals (%)*
Micronycteris megalotis (Gray, 1842)	ins	1 (0.4)
Carollia perspicillata (Linnaeus, 1758)	fru	59 (21.6)
Artibeus fimbriatus (Gray, 1838)	fru	19 (7.0)
Artibeus jamaicensis (Leach, 1821)	fru	5 (1.8)
Artibeus lituratus (Olfers, 1818)	fru	177 (64.8)
Chiroderma villosum (Peters, 1860)	fru	1 (0.4)
Sturnira lilium (E. Geoffroy, 1810)	fru	5 (1.8)
Vampyressa pusilla (Wagner, 1843)	fru	2 (0.7)
Desmodus rotundus (E. Geoffroy, 1810)	hem	4 (1.5)
Total		273

Diet: ins, insectivore; fru, frugivore; hem, sanguinivore.

species were frugivorous, with *A. lituratus* and *C. perspicillata* comprising 86.4% of the total captures (Table 1).

We collected 123 fecal samples from six species of fruit-eating bats: *A. lituratus* ($n = 76$), *C. perspicillata* ($n = 32$), *A. fimbriatus* (Fringed fruit-eating bat) ($n = 9$), *S. lilium* (Little yellow-shouldered bat) ($n = 4$), *A. jamaicensis* (Jamaican fruit-eating bat) ($n = 1$) and *V. pusilla* (Southern little yellow-eared bat) ($n = 1$). From these samples, we recorded 4,139 seeds of different plant species (Table 2). The mean number of seeds per sample was 33.7 ± 85.5, but the majority of these samples ($n = 104$; 74.8%) contained seeds from a single plant species. On the basis of comparisons with a reference collection, we were able to identify seeds from 15 plants to the species level, two to the genus level, and one to the family level (Table 2). These samples encompass plants from three successional categories, with the largest proportion (73.3%) belonging to pioneer species (trees and shrubs).

Discussion

Our initial hypothesis that units with fruit odor would have more movement of fruit-eating bats around them was confirmed. The capture and diet data showed a community rich in frugivorous phyllostomids, which have the potential to disperse a great number of seeds of several plant species around the IU.

Our results corroborate previous studies that verified the efficiency of essential oils by means of tests with artificial fruits attached to mist-nets, inside and outside forest fragments (Mikich et al. 2003; Bianconi et al. 2007, respectively). Mikich et al. (2003) showed that *C. perspicillata* responded strongly to the oil of *P. gaudichaudianum*, even

Table 2. Plant species, successional categories, and seed number (relative frequency) registered in fecal samples from six species of fruit-eating phyllostomid bats captured in the forest area (PVR) between August 2006 and July 2007.

		Seeds per Bat Species^a (%)					
Plant Species	*Successional Categories^b*	*A.l.*	*C.p.*	*A.f.*	*A.j.*	*S.l.*	*V.p.*
Cecropiaceae							
Cecropia glaziouii Sneth.	PI	12.0	0.2				
Cecropia pachystachya Trécul	PI	16.7	0.1	60.1			
Moraceae							
Ficus glabra Vell.	ES	18.6		4.1			83.3
Ficus guaranitica Chodat.	LS	11.2	0.8				
Ficus insipida Willd.	NC	19.6	0.1				
Ficus luschnathiana (Miq)	ES	4.6					
Ficus monckii Hass.	NC	4.7		31.7			
Maclura tinctoria (L.)	ES	2.1	0.3	1.0	100.0		
Solanaceae							
Solanum argenteum Dunal	PI		0.1				
Solanum caavurana Vell.	PI	10.2	2.7				
Solanum sp.	PI		0.6				
Passifloraceae							
nonidentified	NC					22.7	
Piperaceae							
Piper amalago L.	PI		0.2				
Piper crassinervium H.B. & K.	PI			2.6			
Piper diospyrifolium Kunth	PI		0.1				
Piper gaudichaudianum Kunth	PI	0.2	70.9			72.7	
Piper hispidum Sw.	PI	0.1	23.9			4.6	16.7
Piper sp.	PI			0.5			
Seeds Total (n)		1,639	2,230	193	5	66	6
Samples Total (n)		76	32	9	1	4	1

^{a} Respectively: *Artibeus lituratus, Carollia perspicillata, A. fimbriatus, A. jamaicensis, Sturnira lilium* e *Vampyressa pusilla.*

^{b} Successional category (cf. Gandolfi et al. 1995): PI, pioneer; ES, early secondary; LS, late secondary; NC, no classification (Gandolfi et al. 1995; Martins & Rodrigues 2002; Cardoso-Leite et al. 2004; Martins et al. 2004; Rodrigues et al. 2005; Hardt et al. 2006).

with a high availability of alternative resources in the environment. On the other hand, Bianconi et al. (2007), using oils from *P. gaudichaudianum, P. crassinervium* and *Ficus insipida* in agricultural fields, attracted mostly *A. lituratus*, independent of the oil used. In this case, the authors suggested that in areas where food resources are scarce bats might be attracted by the smell of fruits that might not be necessarily their preferred ones. They also pointed out that the majority of captured animals had seeds from several plant species in their feces, thus validating the potential of this technique to restore degraded areas.

Which bat species responds better to the oils in open areas, away from forests? Bianconi et al. (2007) reported the capture of six frugivorous species (*A. lituratus, A. jamaicensis, A. fimbriatus, S. lilium, C. perspicillata,* and *Chiroderma villosum* [airy big-eyed bat]) in nets treated with essential oils in agricultural fields (soy and corn). According to the authors, the attraction in these areas is associated with species-specific foraging patterns, with higher captures recorded for those species that include frequent movement between forest fragments. A long-term (7 yr) and wide-scale (10 forest fragments) study indicated that some phyllostomids (including *Artibeus* spp. and *C. perspicillata*) continually crossover agricultural areas (Bianconi et al. 2006). This tendency has also been found in fragmented habitats in Mexico, Costa Rica, Nicaragua, and the Central Amazon, including other representatives of the Stenodermatinae and Carollinae subfamilies (*S. lilium*, several species of *Artibeus* and *Carollia*—Galindo-González et al. 2000; Estrada & Coates-Estrada 2002; Bernard & Fenton 2003; Medina et al. 2007; Kelm et al. 2008).

The high mobility shown by some species of bats is related, among other factors, to the availability of food in the landscape (Heithaus et al. 1975; Morrison 1978). For example, individuals of *Sturnira* and *Carollia* that respond to the fruiting patterns of Solanaceae and Piperaceae respectively (Fleming 1988; Mello et al. 2008), may visit different forest fragments (Bianconi et al. 2006; Medina et al. 2007) in order to find food. In other cases, day or night roosts were located at strategic locations in the area, many times in the midst of abandoned fields or pastures (Kelm et al. 2008; Bianconi 2009). As such, there appears to be a strong phylogenetic influence on bat ranging patterns. For example, *Artibeus* species are recognized by their great flying potential and strong preference for *Ficus* spp; they can use large areas to search for food (e.g. Morrison 1978, 1980). If we consider that fig trees are found in low densities and that they have fruit asynchronously (Morrison 1978), offering a great quantity of fruit for a short period of time (Kalko et al. 1996), we should expect frequent mobility of *Artibeus* spp. in fragmented forests (Bianconi et al. 2006).

Even though our experiments do not reveal clearly which species were attracted to the IU, the flight patterns observed coincide with those previously described for frugivorous Phyllostomidae. For example, exploratory movements (search) and approaches to the food in concentric circles (independent of whether the item is manipulated or not) are well documented for Stenodermatinae and Carollinae subfamilies (for instance, *C. perspicillata, C. castanea* (Chestnut short-tailed bat) H. Allen, 1890*, Artibeus* spp., *V. pusilla*), in natural conditions and in captivity (Kalko et al. 1996; Thies et al. 1998; Korine & Kalko 2005). The bats' positive response to the olfactory stimulus (oiled septum) reinforces the importance of the sense of smell as the main sense used by some species to locate ripe fruit (Thies et al. 1998; Korine & Kalko 2005; Mikich et al. 2003; Bianconi et al. 2007). Additionally, it is worth noting that because these species fly around the source of smell for a relatively extended period of time, there is likely to be an increase in the probability of dispersing seeds in the area.

The capture data presented in this study are directly related to the practical and functional characteristics of the tool, as they indicate a rich taxocenosis in frugivorous bats. The dominance of *A. lituratus* and *C. perspicillata* (together accounting for 86.4% of total captures), followed by other frugivorous Phyllostomidae (*A. fimbriatus*, *A. jamaicensis,* and *S. lilium*), agrees with findings from several other Atlantic Forest fragments (e.g. Reis & Muller 1995; Pedro et al. 2001). Our results were also similar to those found in similarly fragmented neotropical ecosystems, where the frugivorous guild is also dominated by Stenodermatinae and Carollinae (e.g. Schulze et al. 2000; Estrada & Coates-Estrada 2002; Willig et al. 2007).

The majority of captured bats had seeds in their feces, mostly from pioneer species, which are known to act as facilitators in the colonization process of secondary species (Muñiz-Castro et al. 2006). Additionally, the establishment of pioneer species in isolated areas may also increase the zoochoric seed rain by other volant vertebrates, as usually observed for isolated trees in pasture and agriculture matrix (e.g. Guevara & Laborde 1993; Galindo-González et al. 2000).

The plants consumed were in agreement with previous studies of the species diet (e.g. Acosta y Lara 1950; Aguiar & Marinho-Filho 2007; Silva et al. 2008), including our study area (Mikich 2002). *Artibeus* spp. has a known preference for fruits of Cecropiaceae and Moraceae, whereas *C. perspicillata* prefers fruits of Piperaceae (August 1981; Charles-Dominique 1986; Kalko et al. 1996; Thies & Kalko 2004). There is increasing evidence that relations like these contribute to the regional distribution and genetic structure of plant species, thereby influencing the population dynamics and diversity of neotropical forests (Galindo-González et al. 2000; Garcia et al. 2000).

Thus, considering: (1) the effectiveness of essential oils in attracting bats to pastures and agricultural fields, (2) the composition of frugivorous Phyllostomidae (species and individuals) in forest fragments, and (3) their foraging behavior, diet and, seed dispersal potential, we conclude that the essential oils of chiropterochoric fruit increase the quality and quantity of seed rain in predefined sections of agricultural and pasture areas. The use of such attractants would make bats spend time around the source of smell, defecating seeds that are important in the forest successional process. This technique has great potential for natural methods of regeneration assisted by dispersers and, consequently, for the recovery of certain parts of the Atlantic Forest, such as riparian forests or reserves and protected areas that need to reforest agricultural or pasture areas. Moreover, because frugivorous bats are widely distributed, the technique has the potential to be used around the world to recover degraded forests.

Implications for Practice

- This technique has the potential to be used as a natural method of forest regeneration, either alone or together with other restoration techniques (e.g. sowing of seeds, planting seedlings, or using other nucleation techniques).
- The successful deployment of this approach will depend on the presence and proximity of neighboring areas (e.g. forest fragments) as sources of both bats and propagules.
- Owing to interspecific differences in fruit preferences the effectiveness will also depend on prior knowledge of the species composition of bats in the source area and the temporal variation in fruit availability.
- As any other technique that depends on seed dispersers there are some drawbacks such as potential limitations resulting from the dispersal of preferred species independent of the capacity of the seed to establish or the invasion potential.
- Before the compounds responsible for bat attraction could be identified and synthesized the large use of the essential oils could compromise fruit availability for frugivores.

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