Roads as barriers to seed dispersal by small mammals in a neotropical forest

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Abstract: We sought to answer the question of whether tropical forest roads act as barriers to seed dispersal by small mammals. Ten paired seed stations were placed 100 m apart along the first 2 km of Pipeline Road in Soberanía National Park, Panamá, with each station containing 5 Astrocaryum standleyanum and 5 Attalea butyracea fruits with intact seeds. An industrial sewing bobbin was attached to each seed to allow movement to be tracked. We observed 154 seed movements; maximum distance moved was 20 m, with a mean of 5.75 m (SD = 5.19). More A. butyracea (131) were moved than A. standleyanum (23), and removal rates varied among the 10 stations. Although some seeds were moved sufficiently far to have crossed the road, none were, indicating that roads do act as barriers to seed dispersal in neotropical forests and that continued expansion of road networks into tropical forests may threaten biodiversity.

Resumen: Nosotros tratamos de responder a la pregunta de si los caminos en los bosques tropicales actúan como barreras para la dispersión de semillas por mamíferos pequeños. Se colocaron 10 estaciones pareadas a intervalos de 100 m a lo largo de los dos primeros kilómetros del Camino del Oleoducto en el Parque Nacional Soberanía, Panamá. Cada estación contenía cinco frutos de Astrocaryum standleyanum y cinco de Attalea butyracea con las semillas intactas. Se fijó una bobina de costura industrial a cada semilla para permitir rastrear su movimiento. Observamos 154 movimientos de semillas; la distancia máxima de movimiento fue 20 m, con una media de 5.75 m (DE = 5.19). Hubo más movimientos de A. butyracea (131) que de A. standleyanum (23) y las tasas de remoción variaron entre las 10 estaciones. Aunque algunas semillas fueron movidas a una distancia suficientemente grande como para poder haber cruzado el camino, ninguna lo hizo. Esto indica que los caminos sí actúan como barreras para la dispersión de semillas en los bosques neotropicales y que la expansión continua de redes de caminos hacia el interior de los bosques tropicales pueden ser una amenaza para la biodiversidad.

Resumo: Procurou-se responder à questão de saber se as estradas florestais tropicais atuam como barreiras para a dispersão de sementes por pequenos mamíferos. Dez estações pareadas de colheita de sementes foram colocados a uma distância de 100 m ao longo dos primeiros 2 km da estrada Pipeline no Parque Nacional Soberania no Panamá, com cada estação contendo frutos com sementes intactas: 5 de Astrocaryum standleyanum e 5 de Attalea butyracea. Uma bobina industrial de linha de costura foi presa a cada semente para permitir que o seu movimento pudesse ser rastreado. Observou-se 154 movimentos de sementes sendo a
ROADS ARE BARRIERS TO SEED DISPERSAL

Introduction

Tropical forests contain the greatest biodiversity on Earth but are also among the most threatened and least understood ecosystems. Sound conservation and management practices of such forests must be based on a thorough understanding of the ecological system (Leigh & Rubinoff 2005), but the general lack of such knowledge has long hindered conservation efforts. Of particular importance is an understanding of the origin and maintenance of tree diversity. While numerous factors are certainly involved in driving and maintaining tropical diversity, recent experimental studies have highlighted the importance of negative feedback imposed by species-specific pathogens in structuring forest communities (Comita et al. 2010; Mangan et al. 2010). Such studies highlight the importance of seed dispersal in maintaining the high levels of biodiversity in tropical forests (sensu Connell 1971; Janzen 1970).

Although tropical trees employ a wide variety of dispersal mechanisms, a high proportion of them are reliant on animal dispersers (Howe & Smallwood 1982), including small granivorous and frugivorous rodents. These animals may play crucial roles in forest regeneration through their actions as seed dispersers and predators (Adler 1995; Adler & Kestell 1998; Asquith et al. 1997; Hoch & Adler 1997; Lambert et al. 2005; Struhsaker 1997; Terborgh et al. 2001). In fact, studies in both the Old and New World tropics have documented completely-suppressed forest regeneration after disturbance, an effect at least partially attributable to increased small mammal abundance and consequent seed predation (Struhsaker 1997; Terborgh et al. 2001). Numerous studies have documented the effects of large-scale disturbance, such as fragmentation and logging, on small mammal communities and seed dispersal (Lambert et al. 2003; Lambert et al. 2005; Struhsaker 1997; Terborgh et al. 2001). However, to date no studies have examined the impacts of smaller-scale disturbances such as road construction in tropical forests. Given the continuing expansion of road networks in many tropical regions, such studies are urgently needed (Laurance 2006; Skole & Tucker 1993).

Studies conducted in temperate forests indicate that even unimproved roads can greatly impact ecosystems by fragmenting habitat, providing sources of mortality, and acting as barriers to animal movement (Arima et al. 2005; Forman & Alexander 1998; Spellerberg 1998; Swihart & Slade 1984). Roads that disrupt animal movement can influence density and home range size (Clevenger et al. 2003; Marsh et al. 2005; McDonald & St. Clair 2004; McGregor et al. 2008). Furthermore, roads create edge habitat, which can profoundly affect animal communities (Lovejoy et al. 1986).

If tropical small mammals respond to roads in manners similar to their temperate counterparts, then the expansion of road networks in the tropics could disrupt seed dispersal patterns by either changing the movement patterns of small mammals or affecting how and where mammals disperse and cache seeds. Such disruption may limit the ability of seeds to gain access to suitable areas in which to germinate, which in turn may hinder forest regeneration, thereby ultimately affecting biodiversity. In this study, we sought to answer the question of whether tropical forest roads act as barriers to seed dispersal by small mammals.

Materials and methods

The study was conducted along Pipeline Road in Soberanía National Park (9°10’N, 79°45’W), a 22,000-ha tract of tropical moist forest in central Panamá. Pipeline Road runs from southeast to

distância máxima dos mesmos de 20 m, com uma média de 5,75 m (SD = 5,19). Mais sementes de A. butyracea (131) foram movimentadas do que para a A. standleyanum (23), e as taxas de remoção variaram entre as 10 estações. Embora algumas sementes tivessem sido transferidas suficientemente longe para ter atravessado a estrada, nenhuma indicou que as estradas tenham agido como barreiras à dispersão de sementes em florestas Neotropicais e que a contínua expansão das redes de estradas em florestas neotropicais possa ameaçar a biodiversidade.

Key words: Central Panama, forest regeneration, Proechimys semispinosus, roads, small mammals, seed dispersal.
northwest and provides access to second-growth forest that is in various stages of regeneration and patches of old-growth forest. The pipeline and its associated road were constructed during World War II. The road was formerly asphalt but has since degraded to mostly dirt and gravel. Currently, the single lane road (~3m wide) receives periodic maintenance, including grading, and light vehicle and foot traffic (TDL pers obs.). Our study was conducted along the first 2 km of Pipeline Road, at the southern terminus. Forest in this area is mostly early successional (ca. 60 - 100 years old), with canopy heights ranging from ca. 5 - 20 m. This area was selected because younger forests often harbor higher-density small mammal populations than older forests, which would increase the number of seed removal events we could expect (Lambert & Adler 2000) and because such forests are actively regenerating from past widespread disturbances (e.g., logging and pasturage).

Elevation along the road ranges from ca. 40 - 200 m (Karr 1990), and the annual rainfall ranges from a mean of 2188 mm at the southern terminus of the road, where the study was conducted, to 2685 mm at the northern terminus (Windsor 1990). The area is highly seasonal and experiences a pronounced four-month dry season from January through April, during which <10 % of the annual precipitation occurs. The seasonal patterns in rainfall produce distinct patterns in fruit and seed availability (Adler & Lambert 2008; Lambert & Adler 2000). The project was conducted at the start of the rainy season (June & July) in 2009 (55 nights) and 2010 (45 nights), utilizing two stations. Stations were placed within the forest exposed) for a total of 10,000 fruit nights (5,000 for A. standleyanum and 5,000 for A. butyracea) where fruits range in length between 2.5 - 6 cm and 3 - 4.5 cm in diameter, whereas A. butyracea fruits are least 4.5 - 8.5 cm long and 3 - 4.5 cm in diameter (Henderson et al. 1995). Both species typically fruit when the study was conducted, with A. standleyanum fruit production generally peaking slightly earlier than that of A. butyracea (Adler & Lambert 2008).

Results and discussion

During the course of the study, fruits were presented for 55 nights in 2009 (six 5-day trials exclosed; five 5-day trials exposed) and 45 nights in 2010 (four 5-day trials exclosed; five 5-day trials exposed) for a total of 10,000 fruit nights (5,000 for A. standleyanum and 5,000 A. butyracea) where one fruit presented for one night equals 1 fruit night. A total of 154 seeds were moved (23 A. standleyanum and 131 A. butyracea). None of these seeds were moved across Pipeline Road. Of the 154 removed seeds, 33 were taken into
subterranean burrows where germination would not be successful; the remainder of the removed seeds were cached under leaf litter where they could presumably regenerate. The maximum distance moved was 20 m, with a mean distance of 5.75 m (SD = 5.19). More seeds (89 total; 3 A. standleyanum and 86 A. butyracea) were moved in 2010 than in 2009 (65 total, 20 A. standleyanum and 45 A. butyracea). In addition to the seeds that were moved, 37 total seeds (18 A. standleyanum and 19 A. butyracea) had their fruit consumed without the seed being removed from its original location. The presence of the exclosures did not affect removal rates (F = 0.30, d.f. = 8, P = 0.11), A. butyracea had higher removal rates than A. standleyanum (F = 8.71, d.f. = 8, P = 0.0043) and seed removal rates differed among the 10 sites (F = 3.42, d.f. = 8, P = 0.0016). All removed seeds followed paths along the ground, with none being transported into the canopy or subcanopy.

Despite recording 154 total seed movements, including 54 seeds that moved ≥ 7 m farther than the distance across Pipeline Road (Fig. 1), no seeds were moved across the road. These observations are in contrast to our concurrent observations of the key seed-dispersing rodents in the study area. Not only did we frequently observe agoutis crossing the road during the day, but trapping and tracking studies (J. Dittel unpublished data) revealed that P. semispinosus also crossed the road at night. These observations indicate that even unimproved, infrequently-travelled roads may act as barriers to seed dispersal and thus may hinder forest regeneration and ultimately pose a threat to biodiversity. The ability of roads to limit seed dispersal could be especially problematic in areas where road expansion leads to habitat degradation and fragmentation through logging, over hunting, and agriculture. In these areas, seeds produced in the few remaining tracts of intact forest may not cross even small barriers to colonize degraded habitat, leading to a gradual but continual loss of biodiversity from the landscape.

The observation that the key seed-dispersing rodents often crossed the road but never carried seeds with them is consistent with road effects in temperate areas, where roads disrupt home ranges, with the road often acting as one boundary of an individual’s home range (Clevenger et al. 2003; Marsh et al. 2005; McDonald & St. Clair 2004; McGregor et al. 2008). Because the rodents are moving seeds, often to cache them for later consumption, it follows that they would deposit such seeds within their home ranges. Although the road likely represents habitat that would be inhospitable to seed caching, studies employing similar methods (Kilgore et al. 2010) found cache locations to be non-random. Therefore, within the forest seeds are often carried through habitat unsuitable for caching. Furthermore, the lack of cover on the roads represents areas of high predation risk for the seed-dispersing rodents. Thus, while the rodents may be willing to cross the road, they are less likely to do so while burdened with seeds. Indeed, we tracked numerous seeds that moved toward the road, but all of those were dropped by the removal agent at the road’s edge, perhaps indicating that the rodent crossed the road after dropping the seed.

In central Panama, smaller spiny rats and squirrels and larger agoutis move and cache seeds (Adler & Kestell 1998; Carvajal & Adler 2008; Flagel et al. 2009; Forget & Milleron 1991; Hoch & Adler 1997). However, little is known concerning the relative importance of those two size classes of seed dispersers. We examined relative removal rates by the two size classes by alternating between having seeds under exclosures that excluded agoutis and exposed seeds that allowed access by all three species. Similar removal rates of the exclosed and exposed seeds indicate that spiny rats or squirrels were the primary seed removal agents and both apparently scatter-hoarded seeds. Thus, smaller seed dispersers must be considered in seed-dispersal models. However, it is likely that...
the relative importance of these species in seed dispersal varies across the landscape. Kilgore et al. (2010) used similar methods near our study site and found that S. granatensis would frequently remove seeds from the ground and carry them into the canopy or subcanopy. However, all of tracked seeds moved along the ground, with none being brought into the canopy or subcanopy, (Kilgore et al. 2010), indicating that in this study P. semispinosus was the primary dispersal agent. Carvajal & Adler (2008) found that seed removal by S. granatensis was higher in areas of intact forest than forest gaps; as all of our seed stations were in the forest edge along the road, it is possible S. granatensis avoided these areas. Removal rates in our study varied among the sites, further indicating that the local abundance of small mammals directly influenced removal rates. Together, these results indicate that the relative importance of various mammalian dispersal agents varies across the landscape.

We also observed higher removal rates for A. butyracea than for A. standleyanum. Previous studies (Flagel et al. 2009; Kilgore et al. 2010) also documented more removals for A. butyracea. However, those studies did not simultaneously present removal agents with both seeds. Therefore, previous studies suggested that the greater number of A. butyracea removals was the result of those fruits tending to be available later in the rainy season when other fruits were less abundant. By contrast, our results indicate that A. butyracea is in fact preferred by the small mammals, a result likely attributable to the higher nutritional value and larger size of A. butyracea (Henderson et al. 1995).

In summary, our results support the findings that small mammals play important roles in tropical systems, acting as seed dispersers and seed predators (Adler 1995; Adler & Kestell 1998; Asquith et al. 1997; Hoch & Adler 1997; Lambert et al. 2005; Struhsaker 1997; Terborgh et al. 2001). Furthermore, our findings suggest that at least in certain microhabitats, smaller rodents such as P. semispinosus may play a larger role in dispersal than larger rodents such as D. punctata. Most importantly, we found that roads do in fact act as barriers to seed movement because despite documenting 154 seed movements, we observed no seed being dispersed across the road. Thus, expanding road networks into tropical forests could limit seed dispersal and ultimately present a subtle yet potentially significant threat to the long-term maintenance of biodiversity in fragmented landscapes. This effect is particularly important given the patchy and over-dispersed spatial distribution of many species of neotropical trees (Hubbell 1979).

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