Pine seed removal in three temperate plant communities

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Abstract

Background: Foraging strategies may vary among guilds of granivores and impact the tree recruitment and biodiversity of plant communities.

Hypothesis: The hypotheses were: during the night in areas with tree cover rodents will be the main seed removers, insects in open areas at night, and birds in all types of plant communities during the daytime.

Mathematical model: The seed removal by birds, rodents and insects was studied in a Mexican temperate forest. In order to detect differences in seed removal of *Pinus patula*, *P. pseudostrobus*, *P. teocote* and *P. montezumae*, a GLMM model with three way interaction (type of plant community, exclusion treatment and period) was carried out for each pine seed species where random variables were the variation among sites and months.

Study site and years of study: This study was carried out in a Mexican temperate forest during February 2006 and January 2007.

Methods: Through exclusion treatments we evaluated the seed removal of four pine species in three plant communities with two replicates (1 ha approximately) and two periods.

Results: The three-way interaction was significant for all pine species ($P < 0.001$) (GLMM processes). The variance was greater among sites than between months. The main seed removers for all pine seed species, were: At night insects for subalpine grassland; during the daytime birds for all plant communities, and at night the rodents in pine forest, oak-alder forest and finally in the subalpine grassland.

Conclusions: The rodents were the main seeds removers in areas with tree cover during the night, the insects in open areas at night, and birds in all plant communities during the daytime.

Key words: birds, daytime and nighttime removal, insects, rodents, tree cover

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Remoción de semillas de pinos en tres comunidades vegetales templadas

Resumen

Antecedentes: Las estrategias de forrajeo pueden variar entre granívoros e impactar el reclutamiento de árboles y la biodiversidad de comunidades vegetales.

Hipótesis: Las hipótesis fueron que: durante la noche en áreas con cobertura arbolada los roedores serán los principales removedores de semillas, los insectos en áreas abiertas en la noche; y las aves en todos los tipos de comunidades vegetales durante el día.

Modelo matemático: La remoción de semillas por aves, roedores e insectos fue estudiada en un bosque templado mexicano. Con el fin de detectar diferencias en la remoción de semillas de *Pinus patula*, *P. pseudostrobus*, *P. teocote* and *P. montezumae*, un modelo GLMM con interacción de tres vías (tipo de comunidad vegetal, tratamiento de exclusión y periodo) fue llevado a cabo para cada especie de pino, donde las variables aleatorias fueron la variación entre sitios y los meses.

Sitio de estudio y año de estudio: Este estudio fue llevado a cabo en un bosque templado mexicano durante Febrero 2006 a Enero del 2007.

Métodos: Mediante tratamientos de exclusión nosotros evaluamos la remoción de semillas de cuatro especies de pinos en tres comunidades vegetales con dos replicas (1 ha aproximadamente) y en dos periodos.

Resultados: La interacción de tres vías fue significativa para todas las especies de pinos ($P < 0.001$) (proceso GLMM). La varianza fue mayor entre sitios que entre meses. Los principales removedores de semillas para todas las especies de pinos, fueron: en la noche los insectos para el zacatal subalpino, durante el día las aves para todas las comunidades vegetales y en la noche los roedores en el bosque de pino, bosque de encino-ilite y finalmente para el zacatal subalpino.

Conclusiones: Los roedores fueron los principales removedores de semillas en áreas con cobertura arbolada en la noche, los insectos en áreas abiertas en la noche, y las aves fueron similares en todas las comunidades vegetales durante el día.

Palabras clave: aves, cobertura arbórea, insectos, roedores, remoción diurna y nocturna.

Seeds are one of the main ways for tree recruitment and the establishment potential in open areas (Perry 2009, Pensado-Fernández *et al*. 2014). They also represent an important habitat and food resource for birds, insects and rodents (Crawley 2000, Kelt *et al*. 2004), which differ spatially and temporally in their foraging strategies (Hulme & Kollmann 2005). For example, during the daytime birds can move among different habitats in search for food resources because of their flight ability (Flores-Peredo 2005), while rodents during the night do so in places with tree cover where the availability of food resources is greater (Hulme & Kollmann 2005, Chung & Corlett 2006, Flores-Peredo *et al*. 2011) and the predation risk by carnivores is lower (LoGiudice & Ostfeld 2002). However under high risk, rodents also use open areas for foraging, but stay near wooded areas if they require shelter (Whelan *et al*. 1991). Insects can be spatially more limited because they avoid sites with dense vegetation that represents an obstacle in seed removal (Crist & Wiens 1994, Notman & Villegas 2005) and prefer to remove seeds during the night because during the daytime the soil temperature is higher (Crist & MacMahon 1991).

The granivores can influence the regeneration, composition and structure of different plant communities because they show food preferences (Flores-Peredo *et al*. 2011). The removal is motivated by seed traits such as the nutritional quality, size and the presence of secondary compounds that vary among a large number of plants (Shimada & Saitoh 2003, Hulme & Kollmann 2005, Wang *et al*. 2012), including pines (Lobo *et al*. 2009), and intervene in their evolution process (Hulme & Benkman 2002). In temperate forests, rodents exert a significant impact on the establishment and permanence of different pine species (Briggs *et al*. 2009). Pines carry out their seed dispersal processes during the dry season March-June (Perry 2009, Cortés-Flores *et al*. 2013) and the phenological overlap among them occur (Hulme & Kollmann 2005, Martínez & González-Taboada 2009), while in subalpine grassland the seed availability is almost all year (Peterson & Rieseberg 1987, Herrera-Arrieta 2007). Other granivores, such as insects and birds, increase the seed removal complexity (Hulme & Kollmann 2005, Flores-Peredo *et al*. 2011, Brigss 2009). The species composition and seed availability determines the movement of granivores among different types of plant communities to find food resources and consequently to impact plant communities (Hoshizaki & Miguchi 2005). Accordingly the interaction between plants and granivores can have reciprocal effects, for example, if the plant composition changes, the structure and composition of granivores also change and vice versa (Meiners & Stiles 1997, Hulme & Kollmann 2005, Notman & Villegas 2005).

Some studies also have examined the effect of the period (daytime vs. nighttime) and type of plant community on seed removal by different types of granivores. For example in arid and semi-arid regions, ants and birds mostly remove seeds during the day, while rodents do so at night (Kelt *et al*. 2004). In open areas in the Mediterranean, during the day ants are the main seed removers while in areas with plant cover the nocturnal rodents are the principal removers (Hulme 1997). Information is still scant for temperate forests in areas with tree cover though, the nocturnal rodents have been documented as the main seed removers (Hoshizaki & Miguchi 2005, Hulme & Kollmann 2005). In this study we evaluated the seed removal for four species of pine trees (*Pinus patula*, *P. pseudostrobus*, *P. teocote* y *P. montezumae*) carried out by three different granivores (rodents, insects and birds) in three temperate plant communities (pine forest, oak-alder forest and subalpine grassland) (Flores-Peredo *et al*. 2011), and two periods (daytime and nighttime). These pine species form adjacent patches to the other types of plant communities. The stage of seed removal study only included those that had already been liberated from the pine cones and dispersed by the wind; i.e. we did not include, for example, seed removal or predation from pine cones by tree-dwelling squirrels. We addressed the following questions: 1) Are pine seeds species removed significantly different among types of granivores, plant communities and daytime-nighttime? 2) Are there interaction among types of granivores, plant communities and daytime-nighttime? Our hypotheses are: a) since the availability of food resources is greater and risk predation by carnivores is less for rodents in areas with tree cover, we expected that at night in these areas, rodents will be the main seeds removers. Also, b) because seed removal by insects can be limited in sites with dense vegetation and a higher soil temperature in open areas, then the insects will remove more seeds in open areas during the night. Finally, c) if the birds can move speedily among different plant communities, then we expect that their seed removal will be similar among all types of plant communities in the daytime.

Methods

Study area. This study was carried out in the central part of the state of Veracruz, in the Ecological Reserve of San Juan del Monte, Veracruz, Mexico between 19° 39' 00"–19° 35' 00" N and 97° 05' 00"–97° 07' 30" W, and between 2,327 and 3,100 m a.s.l., over an area of 609 ha. The climate is mild with frequent cloud cover and frost in winter, with annual temperatures ranging between -3 and 28 °C. There is an annual average rainfall of 1,500 mm, with abundant rainfall in summer and early autumn. The plant community study consists of three temperate plant communities with two replicates: pine forest, oak-alder forest and subalpine grassland, some of which are adjacent to each other, while others are separated by a matrix of subalpine grasslands and shrubs such as *Baccharis conferta* (Compositae height: 1 to 3 m). Pine forests are composed predominantly of *Pinus teocote*, and to a lesser degree *P. patula*, *P. pseudostrobus* and *P. montezumae* (Pinaceae) with heights of 15 to 25 m. Seeds are dispersed between March and June. The distance between trees is 6 to 8 m, and mosses, ferns and plants such as *Alchemilla pectinata* (Rosaceae), *Archibaccharis androgyna* (Asteraceae) and *Pteridium aquilinum* (Hypolepidaceae) grow in the understory. The oak-alder forest is composed of *Quercus crassifolia* (Fagaceae) and *Alnus jorullensis* (Betulaceae), which are 6 to 12 m tall. Fallen leaves decompose and form a layer of organic material on which fungi and mosses grow. Seeds are dispersed also between March and June. The subalpine grassland consists mainly of clumps of *Brachypodium mexicanum* (Gramineae) and *Muhlenbergia macroura* (Poaceae), which grow closely together (1 m) or sometimes with no spacing at all, and form clumps of up to 1 m high, these species are perennial. There are also a few shrubs, such as *Baccharis conferta* (Flores-Peredo & Vázquez-Domínguez 2016).

We randomly selected ten dominant trees from each of four pine species: *Pinus teocote*, *P. patula*, *P. pseudostrobus* and *P. montezumae*. To obtain seeds, we collected 800 mature pine cones (200 per species) during the seed production period (November to January) and prior to seed dispersal.

Seed removal. To assess seed removal we selected two areas of similar topography and size for each of the three temperate plant communities (pine forest, oak-alder forest and subalpine grassland). In each area of approximately 1 ha, 30 experimental units were randomly established, with three access-exclusion treatments in each unit. Each unit consisted of a 16 × 16 cm square, in which a stainless steel mesh measuring 10 × 10 cm was placed. In each of these exclosures, 20 seeds were placed (five seeds per pine species). The experimental units were separated by at least 10 m. There were three access-exclusion treatments with the following characteristics: 1) Ten units only allowed insects to enter, i.e. they excluded birds, rodents and medium-sized mammals with netting measuring 16 × 16 cm, 9 cm tall, and a mesh opening of 0.5 cm; 2) Ten units allowed mice and insects to enter, i.e. they excluded medium-sized mammals and birds with netting measuring 16 × 16 cm, 9 cm tall, with a mesh opening of 2 cm; and 3) Ten control units with free access, i.e., with no mesh and therefore no exclusion. The netting was staked to the ground with four metal stakes, 10 cm long, and was left in place from 0600 to 1800 h (daytime removal) and from 1800 to 0600 h (nighttime removal). To minimize learned behavior principally by vertebrates, each experimental unit was placed randomly (Mares & Rosenzweig 1978). Every 12 h, the number of seeds removed was counted and those missing were replaced. This was done for four days and four nights each month in each vegetation type between February 2006 and January 2007.

Statistical analysis. We assess the normality of data (number of seeds removed) through a Shapiro-Wilk's test (Crawley 2007). Because these data did not assume normality, differences in seed removal for each pine species among three plant communities, daytime and nighttime, and the three exclusion treatments were evaluated using a Generalized Linear Mixed Model (GLMM, Bolker *et al.* 2009, Zuur *et al.* 2009, Wang *et al.* 2012). A Poisson distribution (response variables were counts) and log as link function in the model was used, such as the random effects the two study sites and months, and as the three fixed effects (type of plant community, exclusion treatment and period daytime and nighttime) were considered. The interactions among these

factors were included through a full factorial analysis of the fixed effects (Zuur *et al*. 2009). Significant differences among levels of the explanatory variable were evaluated using the mult-comp package version 1.3–5 (Bretz *et al*. 2010) in the R language (Hornik 2016).

Results

The generalized linear mixed models was significant in the three way interaction (type of plant community × exclusion treatment × period) for all pine seed species *Pinus patula*, df = 4, Wald Stat = 1,157.8, *P* < 0.001, *P. pseudostrobus*, df = 4, Wald Stat = 1,543, *P* < 0.001, *P. teocote*, df = 4, Wald Stat = 799.4, *P* < 0.001 and *P. montezumae*, df = 4, Wald Stat = 871.8, *P* < 0.001. The greatest variance in GLMM models was provided by the sites compared to the months for all pine species *P. patula* (AIC = 22,177.4, Sites 0.085, Months 0.001), *P. pseudostrobus* (AIC = 24,752.2, Sites 0.056, Months 0.002), *P. teocote* (AIC = 17,527.3, Sites 0.082, Months 0.001) and *P. montezumae* (AIC = 18,925.1, Sites 0.107, Months 0.003). Insects were the main seed re-movers of all pine seed species in the subalpine grassland during the night, *Pinus patula* 201.25 ± 27.49; *P. pseudostrobus* 181.75 ± 39.21, *P. teocote* 115.50 ± 29 and *P. montezumae* 60.37 ± 19.32 (Figure 1).

In open access treatment during the daytime the seed removal of all pine species did not differ among types of plant communities suggesting that it was carried out by birds. However during the night the greatest seed removal was carried out in the pine forest and subalpine grassland for all pine seed species, Pine forest (*Pinus patula* 171.62 ± 19.94, *P. pseudostrobus* 184.16 ± 23.11, *P. teocote* 162.41 ± 20.01, *P. montezumae* 141.54 ± 19.71), and Subalpine grassland (*P. patula* 149.87 ± 22.58, *P. pseudostrobus* 130.54 ± 18.47, *P. teocote* 85.08 ± 11.16, *P. montezumae* 84.75 ± 13.53) (Figure 1).

During the night the rodents were the main seed removers in the pine forest followed by oak-alder forest and finally in subalpine grassland for all pine seed species. *Pinus patula* (Pine forest 195.41 ± 20.25, Oak-alder-forest 170.20 ± 18.96, Subalpine grassland 127.54 ± 17.78); *P. pseudostrobus* (Pine forest 210.75 ± 22.39, Oak-alder-forest 164.41 ± 19.15, Subalpine grass-land 110.16 ± 16.71); *P. teocote* (Pine forest 136.58 ± 17.05, Oak-alder-forest 105.20 ± 13.90, Subalpine grassland 68.70 ± 9.81); *P. montezumae* (Pine forest 149.20 ± 18.59, Oak-alder-forest 103.75 ± 14.03, Subalpine grassland 66.87 ± 10.99) (Figure 1).

Discussion

Seed removal per pine species differed among types of plant communities, granivorous group and period; also the interactions among these were significantly different. Our results support those reported by Hulme & Kollmann (2005) mentioning that among guilds of granivores foraging strategies vary spatially and temporarily based on their particular biology as well as features such as size, social structure and movement capacity. However, experimental studies in semi-arid ecosystems reveal marked intercontinental differences in both the overall magnitude of post-dispersal seed predation and the relative importance of different guilds of seed predators. Rodents play a major role in the Northern Hemisphere whereas ants appear more important in the Southern Hemisphere, where overall rates of postdispersal seed predation are considerably lower, whereas in temperate ecosystems they act mainly as seed-dispersers (Hulme & Benkman 2002), an important aspect to consider for the subalpine grassland. Further studies are required to assess how granivory varies across a particular plant species' geographical range.

According to GLMM the sites variation was higher than month's variation. In accordance with Hulme & Benkman (2002), the plant structure among sites are factors that favor different levels of seed removal, because these may vary and impact the activity and temporal patterns of granivores and their effect on the plant recruitment and permanence of vegetation communities. Places with differences plant communities can affect the seed removal rate by vertebrates such as rodents, mammals and birds (Maron & Kauffman 2006), because the seed density is variable (Vander Wall 2010) and likewise the abundance of seed predators (Hulme & Kollmann 2005). In our case differences visibly exist in seed removal among plant communities similar to results documented by the previously mentioned authors.
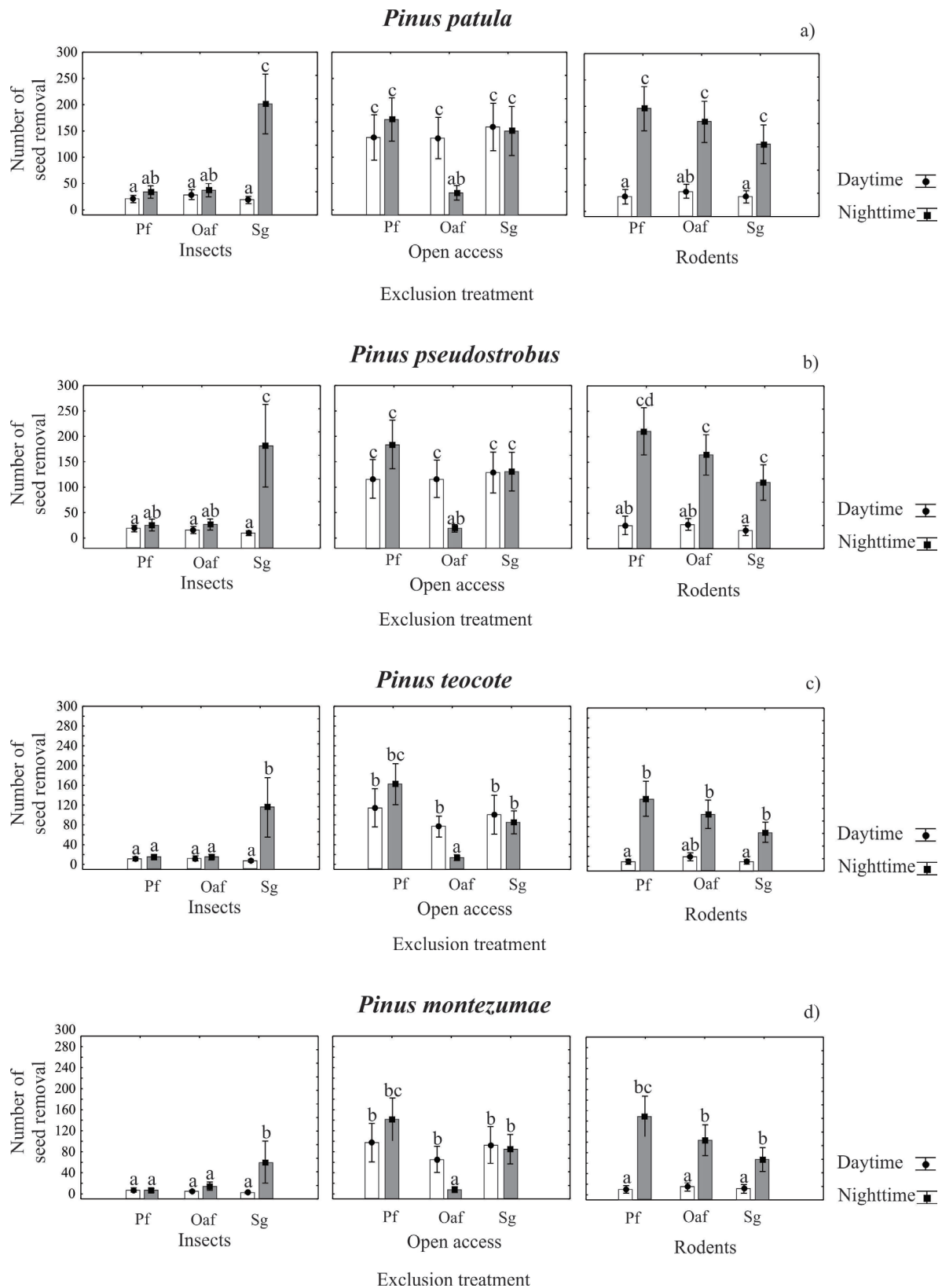
Figure. 1. Differences obtained by generalized linear mixed model of number of seed removal (mean ± SE) for each pine seed species among exclusion treatment, type of plant community and period in a temperate forest in central Veracruz, Mexico. Different letters on the bars indicate significant differences ($P < 0.05$). Pf, Pine forest, Oaf, Oak-alder forest, Sg, Subalpine grassland.

We recorded for all pine seed species a higher seed removal by insects at night in the subalpine grassland versus pine forest and oak-alder forest. In accordance with Hulme (1997) and Hulme & Kollmann (2005) seed removal by insects can be determined by vegetation structure. Trees represent physical barriers that obstruct the movement of seeds by insects increasing the energy expenditure (Crist & Wiens 1994, Notman & Villegas 2005). However, other factors such as seed production phenology (Schafer *et al*. 2006) and high temperatures of the soil during the day in open areas (Briese & Macauley 1980, Sudd & Franks 1987) also are involved. In our study, the subalpine grassland lacked trees, suggesting that during the day the temperatures may have been high because there isn´t arboreal cover and thus shifting the activity of insects to the night when, additionally, the risk of being preyed upon by insectivores is lower (Tigar & Osborne 1999). For colonies of the ant *Pogonomyrmex barbatus* it has been reported that the return of foragers to the nest with food sets from seed removal activity by the entire colony, increasing seed removal rates (Carrol & Janzen 1973, Holldobler & Willson 1990, Schafer *et al*. 2006). This might explain the great number of seeds removed from the subalpine grassland overnight by insects and the permanence of this type of plant community, which is not invaded by the adjacent tree community such as pines, oaks and alder.

At night in the open access treatment, all pine seed species were mostly removed in pine forest and grassland. For the first case, the results may be related with the presence of tree cover where there is lower predation risk by carnivores (LoGiudice & Ostfeld 2002, Hulme & Kollmann 2005) and availability of food resources is greater under the canopy of parent trees (Hulme & Kollmann 2005, Flores-Peredo *et al*. 2011), which increases rates of seed removal by rodents at night. According to this, our results showed that rodents removed more seeds in the pine forest and oak-alder forest followed by open areas, possibly because the subalpine grassland gives them food resources throughout the year (*Muhlenbergia macroura* is a grass species) (Peterson & Rieseberg 1987, Herrera-Arrieta 2007). Besides, for the rodents to forage in open areas they also consider nearby wooded areas to shelter (Whelan *et al*. 1991) such as pine forest and oak-alder forest.

During daytime we did not record differences in seed removal by pine species among types of plant communities. These results could be attributed to the foraging behavior of birds, since their flight ability allows them move speedily among different foraging areas and cover greater distances; birds remove and disperse seeds more than other granivores such as rodents and insects (Wiens 1989, Tigar & Osborne 1999, Ibañez & Soriano 2004, Kelt *et al*. 2004, Milesi *et al*. 2008). This could explain the similar values of seed removal recorded among plant communities during the day, which shows that during the day birds play a pivotal ecosystem function (Muñoz & Cavieres 2006, Whelan *et al*. 2008, García *et al*. 2009). In fact, in the same region Flores-Peredo (2005) also reported that birds were the main removers of *Pinus teocote* seeds during the daytime by direct observation, while rodents were overnight. This coincides with that which was reported for arid and semi-arid environments in Argentina, Chile and Venezuela where birds are also the main seed removers during the day, and small mammals and insects during the night in vegetation remnants and open areas respectively (Marone *et al*. 2000, Kelt *et al*. 2004, Milesi *et al*. 2008).

Finally, assessing differences in seed removal by vertebrates and invertebrates among different plant communities and periods is extremely important, since it permits an understanding of the dynamics of establishment and permanence of plant species and the particular effect of each group of granivores spatially and temporarily (Hulme & Benkman 2002, Hulme & Kollmann 2005).

Conclusions

Rodents were the main seeds removers in areas with tree cover at night, insects in open areas during the night, and birds were similar in all plant communities during the daytime. The interaction with three factors (type of plant community*exclusion treatment*period) was documented.

Acknowledgments

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