PEDECIBA BIOLOGIA
Subárea ZOOLOGÍA
Tesis de Doctorado

Mamíferos en paisajes forestados de Uruguay: diversidad, uso de hábitat y patrones de actividad

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Contenido

Mamíferos en paisajes forestados de Uruguay: diversidad, uso de hábitat y patrones de actividad

Resumen

La forestación constituye una de las principales actividades productivas de Uruguay, que implica la sustitución de ecosistemas naturales, principalmente praderas o pastizales. El objetivo principal de esta tesis de doctorado consistió en la evaluación de los efectos, oportunidades y amenazas que las plantaciones forestales imponen a los mamíferos de Uruguay. Empleando cámaras trampa se relevó la diversidad, el patrón de actividad diario y el uso de hábitat de mamíferos de mediano y gran porte en ambientes insertos en ocho distintos paisajes forestados con *Eucalyptus* del oeste y centro del país (2015-2021; 257 estaciones de muestreo acumulando 22,926 noches/cámara). Para evaluar a escala local los efectos de la forestación sobre la estructura comunitaria, se contrastaron rodales forestales maduros (7-10 años) y cortafuegos (franjas abiertas de 4-8 m entre rodales), con pastizales naturales aledaños, representando estos últimos a los ecosistemas reemplazados. Observamos efectos negativos en la riqueza y uso de hábitat de los mamíferos, especialmente en aquellos de ambientes abiertos, destacándose entre ellos la mulita (*Dasypus septemcinctus*). Sin embargo, varias especies generalistas y omnívoras fueron registrados dentro de componentes forestales, principalmente en los cortafuegos. Estos últimos, podrían además estar cumpliendo un rol como conectores dentro de paisajes forestados, facilitando el tránsito de especies de bosque y de hábitos carnívoros. Para evaluar la variabilidad temporal de los potenciales efectos de la forestación asociados a los cambios fisonómicos y ambientales ocurridos durante el ciclo forestal (0 a 8-10 años), se estudiaron los ensambles de mamíferos en diferentes etapas del ciclo, y su relación con la estructura vegetal. Se observaron fuertes cambios en la riqueza y composición de mamíferos durante el ciclo forestal, con baja diversidad al inicio (0-2 años) y al final del ciclo (7-10 años). En la etapa intermedia (2-4 años) la diversidad fue máxima, y presentó una alta similitud con la observada en bosques nativos. A nivel del paisaje, las ocho áreas con distinto porcentaje de forestación (6-88%) fueron analizadas a distintas escalas espaciales, para evaluar la variabilidad del efecto de las plantaciones sobre los mamíferos. La riqueza de especies prácticamente no varió con el grado de forestación del paisaje, pero la composición específica varió significativamente, dependiendo también de la heterogeneidad ambiental y la cobertura de ambientes naturales presentes. Para especialistas de pastizal, se determinaron umbrales de tolerancia para su persistencia en un paisaje de 5km de radio: entre 70 y 40% de superficie de pastizal remanente. Finalmente, desde el punto de vista temporal circadiano y del ciclo lunar, se evaluaron las diferencias en los patrones de actividad diario de las especies en los distintos grados de forestación y ambientes presentes. En este sentido, importantes diferencias fueron detectadas en los patrones temporales dentro de los ambientes monitoreados, nativos y plantaciones forestales, resaltando nuevamente el uso de los cortafuegos como sitios de paso. En síntesis, esta tesis indica que gran parte de los mamíferos nativos y exóticos, son capaces habitar en paisajes forestados, siempre y cuando se mantengan los ecosistemas nativos circundantes que podrían actuar como fuente de especies. Sin embargo, la respuesta de cada especie fue variable acorde a sus requerimientos de hábitat, dieta y capacidad de adaptación a paisajes modificados, por lo que ninguna medida de conservación será adecuada para todas las especies a la vez. La existencia de variaciones en la actividad diaria de los mamíferos en relación con sol, la luna y los ambientes, podría brindar información relevante para la programación de acciones de manejo en predios forestales, buscando evitar el solapamiento con los picos de actividad de las especies. Los cortafuegos, y la heterogeneidad del paisaje, tanto de ambientes nativos como de etapas de la plantación pueden estar jugando roles clave en el mantenimiento de la biodiversidad dentro de los paisajes, pero las especialistas de pastizal, en particular la mulita (*D. septemcinctus*), necesitan de medidas específicas para su subsistencia en el mediano y largo plazo.

1. Marco General y Estructura de la Tesis

Fundamentación y Antecedentes

Cambios de uso y cobertura del suelo

Unas de las principales causas de la pérdida de biodiversidad a nivel global es el cambio de uso y cobertura del suelo (CUCS), que ha impulsado la fragmentación, degradación y pérdida de hábitats a un ritmo muy acelerado (MEA, 2005; Newbold et al. 2015, 2016; Graham et al. 2019). Décadas atrás, el foco de los programas de conservación estaba en áreas protegidas (Kareksela et al. 2013; Mace 2014; Xavier da Silva et al. 2018), hoy sabemos que esta estrategia es insuficiente para conservar la biodiversidad, y que es clave incluir estrategias de conservación en paisajes productivos (Mace 2014; UNEP-WCMC et al. 2018; Bowyer et al. 2019).

Vinculado a ello, en los últimos años se ha desatado un intenso debate en relación con cuál es la mejor estrategia para compatibilizar la conservación con la producción, que demanda cada vez más tierras productivas para abastecer un consumo creciente. Este debate ha girado en torno a dos estrategias planteadas como alternativas: separación (land-sparing) versus integración de tierras (land-sharing) (Green et al. 2005; Phalan et al. 2011; Fischer et al. 2014; von Wehrden et al. 2014; Kremen 2015; Law and Wilson 2015). La primera aproximación consiste en separar las áreas de conservación (i.e., áreas protegidas) de las áreas de producción intensiva de alimentos y bienes (Green et al. 2005; Fischer et al. 2014). La integración, implica producir y conservar la biodiversidad en las mismas áreas, utilizando métodos de producción amigables con la vida silvestre (Green et al. 2005; Fischer et al. 2014). Para muchos autores, este marco dicotómico no contribuye a la solución de este complejo problema, ya que la conservación y producción sustentable, requiere que ambas estrategias no sean mutuamente excluyentes, sino que trabajen sinérgicamente para equilibrar las necesidades de gestión para la multifuncionalidad de los paisajes (Perfecto and Vandermeer 2012; Grau et al. 2013; Kremen 2015; Grass et al. 2019). Por ende, para promover la conservación en el largo plazo, se necesitan áreas protegidas en los sitios prioritarios para la conservación, pero también, matrices productivas amigables con la vida silvestre, que den como resultado paisajes con conectividad de uso integrado/separado de tierras (land-sharing/sparing conectivity landscape) (Perfecto and Vandermeer 2012; Grass et al. 2019).

En Uruguay, en el marco del importante aumento de las actividades productivas tanto en el sector agrícola, el ganadero y el forestal, existe una gran modificación ambiental, que constituye una amenaza para la conservación de la biodiversidad (Brazeiro et al. 2020). Para poder planificar usos productivos compatibles con la conservación, es esencial evaluar los cambios que éstos provocan y los efectos que tienen sobre el entorno (Fahrig 2003; Fischer and Lindenmayer 2007; Brazeiro 2015;

Decarre 2015; Kshettry et al. 2020) y mejorar la conectividad del paisaje al mantener corredores entre parches de áreas naturales no modificadas (Resasco 2019; Zeller et al. 2020).

Plantaciones forestales

En América del Sur, el CUCS más prominente es la deforestación de bosques tropicales y subtropicales debido al avance de cultivos y áreas ganaderas (Skole and Tucker 1993; Balmford and Bond 2005). Sin embargo, en la región templada del continente (*sensu* Köppen and Geiger 1926), la conversión de pastizales naturales en cultivos y plantaciones forestales ha alcanzado cifras alarmantes, especialmente en la región de los Pastizales del Río de la Plata (PRP, Figura 1-1) (Jobbágy et al. 2006; Baldi and Paruelo 2008; Gautreau 2014; Leidinger et al. 2017). La forestación con especies exóticas para la producción de madera o celulosa es una actividad productiva en expansión mundial, que impulsa la transformación de importantes áreas de tierras naturales, seminaturales o productivas (es decir, bajo otros usos productivos), en plantaciones monoespecíficas (FAO, 2019).

Uruguay, incluido completamente en los PRP, ha experimentado una fuerte expansión de la forestación (géneros *Eucalyptus* y *Pinus*) sobre áreas de pastizal (Figura 1-1). Durante los últimos 30 años, se pasó de menos de 200,000 ha antes de los noventa, a más de 1,000,000 ha en 2013, proyectándose que la superficie forestal llegaría a 2,000,000 ha en 2030 (DIEA-MGAP 2019). Por tanto, la búsqueda de la sustentabilidad del sector forestal es un fuerte desafío, tanto para la autoridad ambiental de Uruguay como para las empresas forestales, y en especial para aquellas que apuntan a la producción responsable y certificación forestal (e.g., Consejo de Administración Forestal - FSC por su nombre en inglés: Forest Stewardship Council; Programa de Reconocimiento de Sistemas de Certificación Forestal- PEFC por su nombre en inglés: Programme for the Endorsement of Forest Certification).

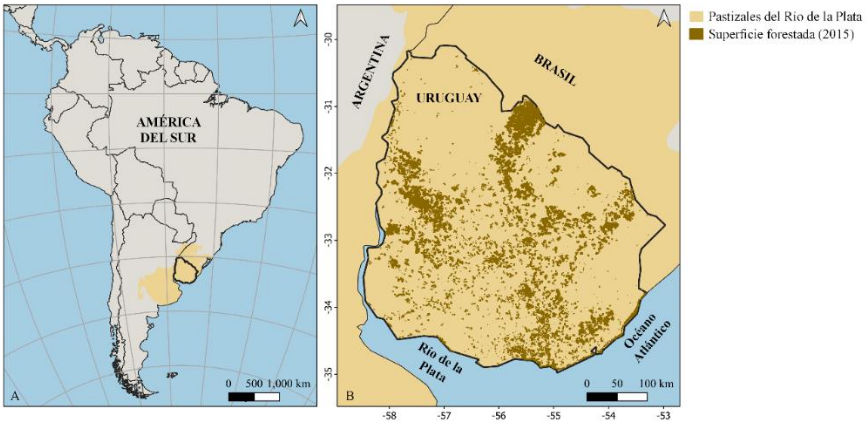

Figura 1-1. Distribución de los Pastizales del Río de la Plata en la región (A) y extensión de la superficie forestal dentro de Uruguay (B).

Implicancias de la forestación

Entre los diversos usos del suelo, el papel funcional de las plantaciones forestales en relación con la conservación de la biodiversidad también se ha debatido fuertemente, confrontándose la visión de que las plantaciones son "desiertos verdes" (e.g., Bremer and Farley 2010; Fischer et al. 2014; Gonthier et al. 2014; Veldman et al. 2015), con la visión de que constituyen hábitats valiosos dentro del paisaje para la flora y fauna nativa (e.g., Crooks 2002; Brockerhoff et al. 2008; Kennedy et al. 2013; O'Callaghan et al. 2016; Law et al. 2017). Diversas revisiones han dejado en claro que las plantaciones forestales no son "desiertos verdes" ya que varias especies, principalmente generalistas, usan este "nuevo hábitat", pero tampoco son comparables a los ecosistemas nativos reemplazados como hábitat para la fauna y flora (Bremer and Farley 2010; Iezzi et al. 2020, 2021). La relación forestación-biodiversidad ha sido relativamente bien estudiada en paisajes dominados por bosques (e.g. Basiron 2007; Dormann et al. 2007; Pawson et al. 2008; Bauhus et al. 2010; Felton et al. 2010; Lindenmayer et al. 2015, 2019; Hua et al. 2016), pero las evaluaciones aún son pocas en paisajes dominados por pastizales (Jobbágy et al. 2006; Andrade-Núñez and Aide 2010; Dotta and Verdade 2011; Lantschner 2012; Veldman et al. 2015; Campos et al. 2018; Iezzi et al. 2020, 2021; Martínez-Lanfranco et al. 2022).

Sin embargo, aunque las plantaciones forestales son cíclicas y no estáticas, la mayoría de las investigaciones sobre los efectos de la forestación se centran en las etapas maduras del ciclo de plantación, mientras que las primeras etapas del ciclo han recibido comparativamente poca atención (Timo et al. 2015; Iezzi et al. 2020; Pairo et al. 2020). La fisonomía vegetal de las plantaciones forestales y su estructura, varían significativamente a lo largo del ciclo forestal (Turnbull 1999; Wagner et al. 2006; Santoandré et al. 2021; Tomé et al. 2021). Por lo tanto, estos monocultivos, a pesar de estar dispuestos simétricamente en el espacio, presentan una importante variabilidad temporal en su estructural (Bormann and Likens 1979; Tscharntke et al. 2012; Riva and Nielsen 2020) que puede afectar la calidad del hábitat para la vida silvestre, afectando la ocurrencia de especies y los patrones de uso del hábitat (Dotta and Verdade 2011; Timo et al. 2015; Iezzi et al. 2020).

Más allá de las plantaciones en sí mismas y su ciclo, la incorporación de la forestación en el paisaje genera mosaicos de distintos tipos de parches, incluyendo rodales forestales (*Eucalyptus* o *Pinus*), cortafuegos, ecosistemas naturales no forestables, en particular bosques (e.g., ribereños, serranos, parques) y parches remanentes de pastizales (e.g., pastizales bajos y rocosos). Según observaciones realizadas por nuestro grupo de investigación, los ecosistemas naturales normalmente ocupan un 30-40% de los establecimientos forestales en Uruguay. La permanencia de estos remanentes nativos podría jugar un rol clave para el mantenimiento de las especies en paisajes forestados, y en particular para aquellas especies más sensibles a los ambientes modificados. Puntualmente, la reducción en superficie de pastizales naturales podría provocar la pérdida local de las especies que hacen uso exclusivo de este hábitat (Iezzi et al. 2020; Cravino and Brazeiro 2021; Martínez-Lanfranco et al. 2022).

La fragmentación en el caso de las plantaciones forestales comprende tanto la pérdida de hábitat como la partición del mismo (fragmentación *per se*), provocando importantes cambios en la configuración de los paisajes (Fahrig 2003; Ewers and Didham 2006). Los efectos de la partición y pérdida de hábitat sobre la integridad ecológica de los paisaje suele ser no-lineal, y puede incluir umbrales críticos de tolerancia (Swift and Hannon 2010) (Figura 1-2). Los umbrales, definidos por puntos de inflexión, son intervalos de transición a través de los cuales pequeños cambios en el patrón espacial producen cambios abruptos en las respuestas ecológicas (Turner and Gardner 1991; With and Crist 1995; Fahrig 2003; Ewers and Didham 2006; Swift and Hannon 2010; Thompson 2011).

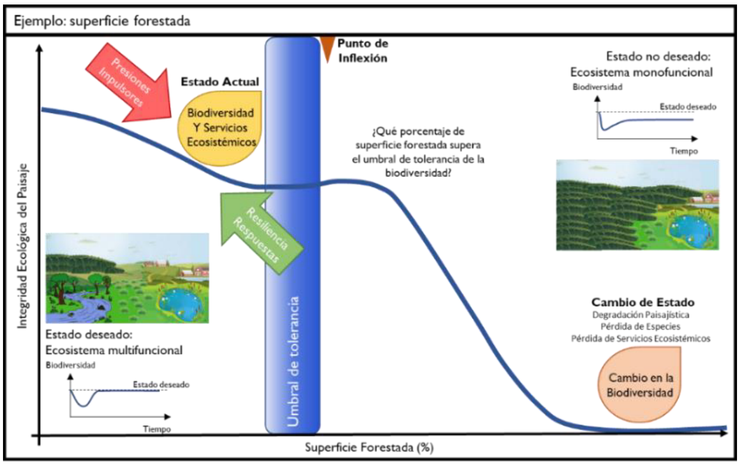

Figura 1-2. Esquema de los umbrales de tolerancia de la biodiversidad dentro de paisajes forestados.

A medida que el paisaje se disecciona y se modifica, la conectividad puede verse interrumpida repentinamente o puede perderse el hábitat original, lo que puede tener consecuencias importantes para la distribución y la persistencia de las especies. ¿Qué niveles de pérdida de hábitat implican la superación de los umbrales de tolerancia? Es una pregunta que continúa abierta dentro de los paisajes forestales en matrices de pastizal. En este sentido, los impactos de las forestaciones sobre la biodiversidad no son generalizables entre los diferentes grupos zoológicos así como tampoco los umbrales (With and Crist 1995; Fahrig 2003; Ewers and Didham 2006), incluso dentro de un mismo grupo, sino que dependen de las especies presentes, de las características de las plantaciones y el entorno natural a múltiples escalas espaciales de evaluación (With and Crist 1995; Fahrig 2003; Fischer and Lindenmayer 2006; Ewers and Didham 2006).

Los cambios comportamentales de las especies dentro de paisajes forestados mencionados hasta el momento, refieren únicamente al nicho espacial del uso de las especies, sin embargo, el nicho temporal no ha sido evaluado en profundidad, sobre todo en plantaciones *Eucalyptus* (Iglesias-Carrasco et al. 2022). El patrón de uso temporal diario es también un descriptor importante del comportamiento de las especies y puede brindar importante información acerca de los determinantes ambientales de la misma (MacArthur and Levins 1967; Schoener 1974; Owen-Smith 1994; Pereira 2010; Wong and Candolin 2015; Iglesias-Carrasco et al. 2022), siendo que los organismos son capaces de modificar los mismos acorde a factores tanto abióticos como bióticos (Schoener 1974; Halle 2000; Colquhoun 2006; Di Bitetti et al. 2009, 2010; Lucherini et al. 2009; Bennie et al. 2014; Maestri and Marinho 2014; Ordiz et al. 2017; Botts et al. 2020b, a; Gallo et al. 2022). El estudio de las distribuciones espaciales y temporales de las especies en predios forestados ayudará a obtener información valiosa sobre su nicho ecológico y para su conservación considerando cómo las especies usan el tiempo, adaptándose a las condiciones y hábitats locales cambiantes (MacArthur and Levins 1967; Schoener 1974; Wong and Candolin 2015; Frey et al. 2017; Iglesias-Carrasco et al. 2022). Las medidas de manejo podrían ser entonces planificadas para evitar el solapamiento temporal con los picos de actividad de las especies, así reducir afectaciones comportamentales (Iglesias-Carrasco et al. 2022).

Mamíferos en predios forestales

Diversos estudios han planteado como los mamíferos responden a las transformaciones antrópicas dentro de los paisajes y ecosistemas (Dotta and Verdade 2011; Fischer et al. 2014; Gonthier et al. 2014; Wong and Candolin 2015; Iezzi et al. 2020; Iglesias-Carrasco et al. 2022). Estas respuestas, no son constantes ni uniformes para todas las especies sino más bien especie-específicas, pudiendo ser positivas, negativas o neutras, siendo sus características y requerimientos biológicos los que influyen sobre el tipo de respuesta, incluso sobre su presencia o ausencia en el sitio (Lindenmayer and Hobbs 2004; Carnus et al. 2006; Fischer and Lindenmayer 2006; Pawson et al. 2008; Bilenca et al. 2017). Es así, que ninguna acción de conservación individual puede beneficiar a todas las especies a la vez y deben considerarse distintas escalas espaciales de análisis.

Los mamíferos, y particularmente los de mediano y gran porte, han sido escasamente estudiados en sistemas de forestación de pastizales (Riffell et al. 2011; Law et al. 2017; Iezzi et al. 2020). Pero juegan un papel importante en los ecosistemas al representar la mayor parte de la biomasa de la vida silvestre (Redford 1992), al ser los principales depredadores y parte de las redes tróficas (Estes et al. 2011; Ripple et al. 2014; Colman et al. 2015) o jugando un papel importante como dispersores de semillas (Howe 1986; Vidal et al. 2013).

Puntalmente en el país, a pesar de la expansión de la actividad forestal a nivel nacional y reconociendo a la misma como una potencial amenaza para la biodiversidad, es escaso el conocimiento que se tiene acerca del impacto de las actividades forestales sobre la estructura de las comunidades de mamíferos (Andrade-Núñez and Aide 2010; Ruiz 2017; Brazeiro et al. 2018). Este tipo de investigaciones podrá brindar insumos para promover la sustentabilidad del sector, permitiendo la conservación dentro de paisajes agroforestales. El manejo efectivo de la biodiversidad en paisajes productivos requiere un enfoque de conservación que integre ambos mundos, el natural y el productivo, pensando en estrategias de conservación que sean especie-específicas.

2. Objetivos

Objetivo general

La presente tesis tuvo como objetivo general evaluar los impactos, oportunidades y amenazas que las plantaciones forestales de *Eucalyptus* imponen a los mamíferos de mediano y gran porte de Uruguay.

El abordaje de este objetivo se realizó enfocando en las siguientes preguntas y objetivos específicos:

Objetivo específico 1

Evaluar el efecto local de la sustitución de pastizales por plantaciones de *Eucalyptus* sobre la diversidad de mamíferos de mediano y gran porte de Uruguay

(1) ¿Cuál es el efecto local (i.e., escala rodal) del reemplazo de praderas sobre la riqueza, composición e intensidad de uso de los mamíferos?
(2) ¿Cómo se relaciona la especificidad de hábitat y trófica con la intensidad de uso de la forestación?

Objetivo específico 2

Evaluar las variaciones en la comunidad de mamíferos a lo largo de las distintas etapas del ciclo forestal de *Eucalyptus*, con relación a los cambios estructurales y ambientales de las plantaciones, en comparación con los ambientes naturales aledaños

(3) ¿Cómo varían estructural y ecológicamente los rodales a lo largo del ciclo forestación en comparación con los ecosistemas naturales (pastizales y bosques nativos)?
(4) ¿Cómo influyen estos cambios sobre la riqueza, composición e intensidad de uso de los mamíferos?

Objetivo específico 3

Evaluar el efecto de la sustitución de pastizales por plantaciones de *Eucalyptus* sobre la diversidad de mamíferos de mediano y gran porte de Uruguay a escala del paisaje.

(5) ¿Cómo responde la diversidad de mamíferos de mediano y gran porte al incremento de superficie forestada dentro de los paisajes?
(6) ¿Cuáles son las especies más sensibles a los cambios de superficie forestada?

Objetivo específico 4

Evaluar el efecto de la sustitución de pastizales por plantaciones de *Eucalyptus* sobre el patrón temporal (según el ciclo solar y lunar) de los mamíferos mediano y gran porte de Uruguay.

(7) ¿Cómo ajustan sus patrones temporales en plantaciones forestales en comparación a ambientes naturales?
(8) ¿Cómo se ven afectados los patrones temporales según el gradiente de forestación?

La tesis doctoral se estructuró en 4 capítulos y un anexo, dentro de los cuales se vinculan los distintos objetivos específicos y sus preguntas. La misma es presentada en formato Tesis por Compendio de Artículos (TCA). Los distintos capítulos fueron formateados en publicaciones para revistas arbitradas específicas de las distintas temáticas, y se presentan en idioma inglés. Una publicación vinculada a hallazgos puntuales se incluye también luego de los mencionados 4. Al final de los artículos a ser referenciados a continuación, se encuentra una discusión general vinculada a los hallazgos.

Publicación 1
Publicado en Forest Ecology and Management, 2021, 484(1), 118937
Grassland afforestation in South America: local scale impacts of *Eucalyptus* plantations on Uruguayan mammals
(*Forestación sobre pastizales Sudamericanos: impactos locales de las plantaciones de Eucalyptus sobre los mamíferos de Uruguay*)
Cravino, A., Brazeiro, A.
URL: https://doi.org/10.1016/j.foreco.2021.118937

Publicación 2
Publicado en Forest Ecology and Management, 2023, 529(1), 120713
Community structure of medium-large mammals across a tree plantation cycle in natural grasslands of Uruguay
(*Estructura comunitaria de mamíferos de mediano y gran porte a lo largo de un ciclo de forestación sobre pastizal en Uruguay*)
Cravino, A., Martínez-Lanfranco, J.A., Brazeiro, A.
URL: https://doi.org/10.1016/j.foreco.2022.120713

Publicación 3
Sometido a Landscape Ecology
Medium-large mammals across a gradient of Eucalyptus plantation cover within Río de la Plata Grasslands
(*Mamíferos de mediano y gran porte a lo largo de un gradiente de cobertura forestal en los Pastizales del Río de la Plata*)
Cravino, A., Martínez-Lanfranco, J.A., Brazeiro, A.

Publicación 4
Sometido a Austral Ecology
Tick, tock… says the moon and the sun: mammals' activity patterns in landscapes with *Eucalyptus* plantation
(*Tic, tac… dicen la luna y el sol: patrones temporales de mamíferos en paisajes con forestación de Eucalyptus*)
Cravino, A., Brazeiro, A.

Publicación 5 (complementaria)
Publicado en Boletín de la Sociedad Zoológica del Uruguay, 2017, 26(1), pp. 23-26.
doi: 10.26462/26.1.5
Ampliación de la distribución del Margay *Leopardus wiedii* (Mammalia: Carnivora: Felidae) en Uruguay
Cravino, A., Brazeiro, A., Fernández, P., Ruíz, M.
URL: https://doi.org/10.26462/26.1.5

Anexo 1. Descripción de los paisajes forestados (caracterización estructural y botánica).

3. Estrategia Metodológica General

Áreas de estudio

Los predios forestales considerados para responder los distintos objetivos corresponden a predios de *Eucalyptus* para la producción de celulosa de la empresa forestal Montes del Plata (MDP). MDP fue fundada en Uruguay en 2009. Su patrimonio territorial está distribuido en trece departamentos del país dentro de la región centro y oeste del país (Figura 3-1). Abarca 134.000 ha forestadas y 87.500 ha de áreas naturales. Dentro de su política de gestión, estableció un compromiso para gestionar sus negocios de manera social, ambiental y económicamente responsable. En este marco, un 96% (212.902 ha) de las áreas bajo gestión de MDP ya cuentan con la certificación FSC de Manejo Forestal Responsable (Montes del Plata 2019).

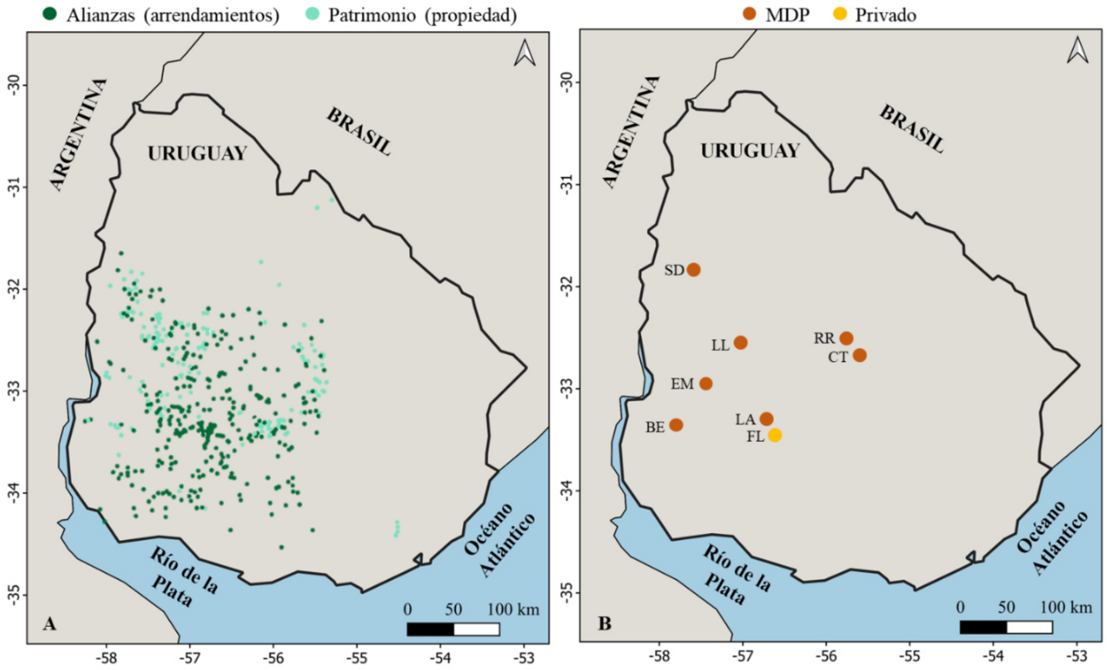

Figura 3-1. (A) Predios manejados por MDP (arrendamientos y propiedades); (B) Ubicación de las áreas de estudio.

Los inicios de este doctorado se enmarcan en una serie de convenios de cooperación entre MDP y Facultad de Ciencias ejecutados entre 2011 y 2017, con el objetivo de apoyar el desarrollo e implementación de una estrategia de conservación de la biodiversidad en predios forestales. Desde 2018 a 2021 los monitoreos fueron llevados a cabo por proyectos de investigación consiguientes.

Dentro del patrimonio de MDP, fueron monitoreados 7 establecimientos cubriendo un gradiente de superficie forestada de 25 a 100% (Cueva del Tigre -CT-, Los Arroyos -LA-, Rincón del Río -RR-, Las Lilas -LL-, El Matorral -EM-, Santo Domingo -SD- y Bequeló -BE-) entre 2015 y 2021 (Figura 3-1). Por fuera de la empresa, se contó con un área de estudio control (Flores -FL-), sin forestación en el entorno de las restantes áreas (2021-2021) (Figura 3-1).

Para la evaluación de los efectos locales correspondientes al capítulo 1 (2015-2017), fueron analizados los establecimientos CT, LA, RR, LL y EM (Figura 3-1). Para la evaluación de los efectos a lo largo del ciclo forestal correspondientes al capítulo 2 (2019-2021) fue analizado el establecimiento SD por presentar amplia heterogeneidad etaria de las plantaciones (Figura 3-1). Para la evaluación de los efectos del paisaje correspondientes al capítulo 3 (2015-2021) y los patrones temporales correspondientes al capítulo 4 (2015-2021), todos los establecimientos fueron considerados (Figura 3-1). Todos los establecimientos realizan forestación para pulpa (i.e., celulosa), sin actividades de raleo o poda (procedimientos de manejo típicos de forestaciones para madera).

A lo largo de estos paisajes, fueron evaluadas las respuestas de los mamíferos a distintas escalas tanto espaciales como temporales (Figura 3-2).

Diseños de muestreo

Para el monitoreo de mamíferos de mediano y gran porte se emplearon cámaras trampa. Las cámaras trampa se han convertido en una de las principales herramientas para el monitoreo de mamíferos de mediano y gran porte a escala global (Burton et al. 2015; Sollmann 2018). La situación en Uruguay no se encuentra muy alejada de dicha situación. Se han abordados temáticas vinculadas al monitoreo de mamíferos en áreas naturales y/o protegidas (Pereira-Garbero et al. 2013; Grattarola et al. 2016) y en áreas productivas (Ruiz 2017; Brazeiro et al. 2018). Distintos proyectos de investigación y tanto tesinas de grado como de posgrado con cámaras trampa se han realizado o se encuentran en desarrollo tanto en este como en el norte del país (Queirolo *com pers*, Farías *com pers,* Alfaro *com pers*).

Puntualmente, para evaluar los efectos de la forestación sobre el ensamble de mamíferos de mediano y gran porte, desde marzo de 2015 a setiembre de 2021 se llevaron a cabo muestreos anuales empleando cámaras trampa (Stealth Cam G42NG) dentro de los mencionados 8 paisajes. Dentro de cada uno de los paisajes considerados se establecieron distintas estaciones de muestreo compuestas por una única cámara trampa. La selección de dichas estaciones fue realizada mediante un diseño aleatorio estratificado con distancias mínimas de separación pre-establecidas, buscando cubrir de forma equitativa la superficie de los ambientes presentes. Para ello, mediante la digitalización de imágenes satelitales (1:5000) se elaboraron capas de base de los usos del suelo de alta precisión en un entorno de 10km del centroide de cada establecimiento.

Cuando presentes, fueron cubiertos tanto ambientes nativos (bosques y praderas) como componentes forestales (rodales de *Eucalyptus* y cortafuegos). Se considera rodal a los bloques de árboles plantados propiamente dichos, y cortafuego a los remantes lineales sin plantar que se encuentran entre rodales. En todos los establecimientos, salvo en SD, las cámaras permanecieron activas durante 90 días y luego rotadas hasta completar un año de monitoreo tanto en ambientes nativos como en plantaciones de edad madura. Puntualmente en SD, las distintas edades del ciclo forestal (recién plantado -Edad

1-, jóvenes -Edad 2-, adultos -Edad 3-, madura pre-cosecha -Edad 4-) presentes fueron monitoreadas de forma continua durante 2 años hasta que cada etapa culminara pasara a la siguiente.

Todos los equipos fueron seteados para tomar 3 fotografías por cada gatillo, con 15 segundos de descanso y sensibilidad alta. La altura de colocación fue de aproximadamente 50cm del suelo, salvo en casos donde existía riesgo de crecida de agua. Detalles específicos de cada diseño y análisis correspondientes se encuentran en las publicaciones que siguen y en su correspondiente material suplementario.

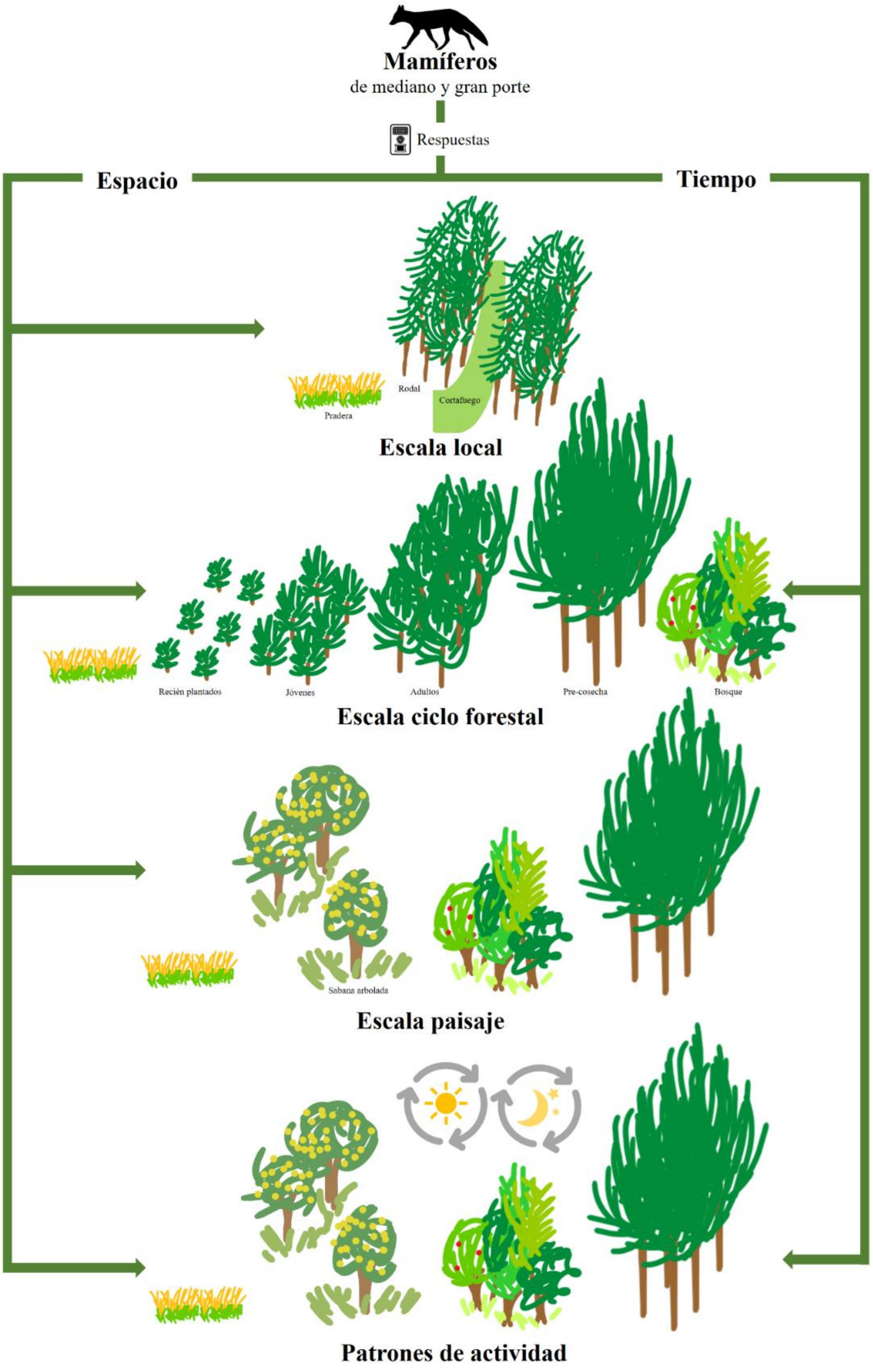

Figura 3-2. Esquema general de escalas espacio-temporales abarcadas por los objetivos específicos.

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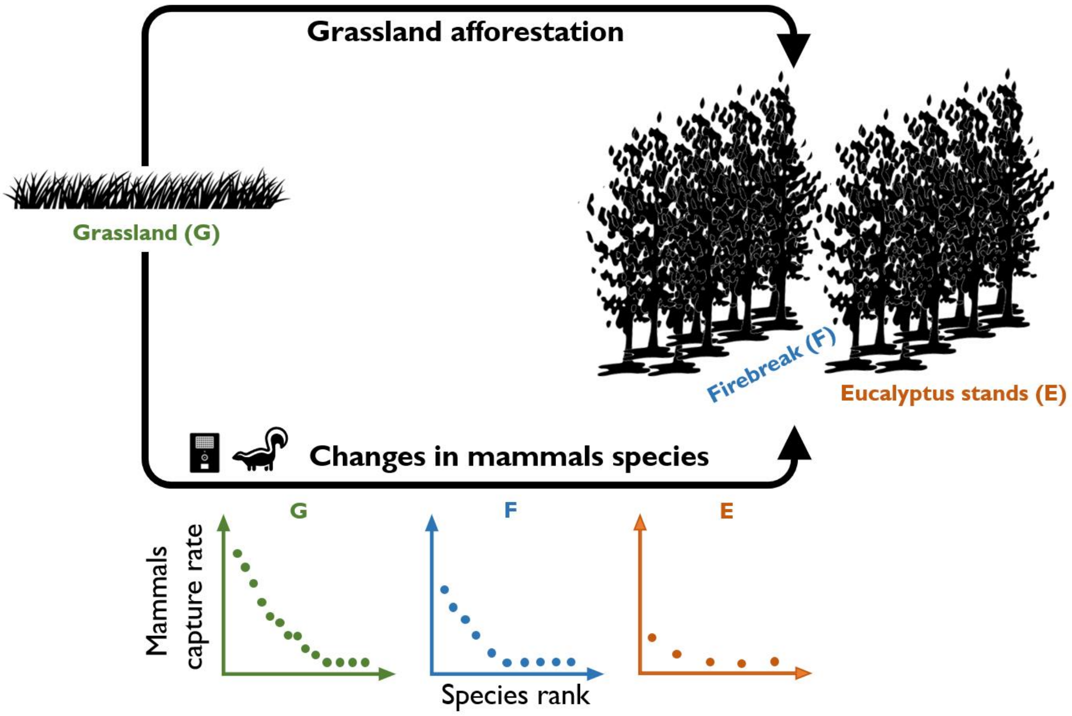
Forestación sobre pastizales Sudamericanos: impactos locales de las plantaciones de *Eucalyptus* sobre los mamíferos de Uruguay



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Grassland afforestation in South America: Local scale impacts of *eucalyptus* plantations on Uruguayan mammals

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ABSTRACT

One of the main causes of global biodiversity loss is the change in land use and land cover, causing fragmentation and habitat loss. Uruguay has experienced a strong expansion of afforestation during the last two decades, at the expense of grasslands. In five afforested landscapes we installed camera traps following a stratified random sampling design covering grassland adjacent eucalyptus and firebreaks to evaluate the effects of grassland afforestation on the medium and large-sized mammal assemblage in Uruguay. We successfully recorded data in 111 sampling stations with a sampling effort of 9043 camera-nights. A total of 14 mammal species were registered, 11 native and 3 exotics. Our results show that grassland afforestation generates a negative impact at a local scale on the assemblage of medium and large-sized native mammals in the five study areas, reducing cumulative species richness and capture rate compared to grasslands. The generalist, omnivore, and insectivore species were the dominants and the only ones detected within the eucalyptus stands, while the grassland specialist in our study, *Dasypus septemcinctus*, was never registered in this environment. On the other hand, the evidence also shows that tree plantations are not "green deserts", since 35% of the species were recorded on the stands, ascending to 70% if the species registered in firebreaks are added. Firebreaks, the linear structures of grasslands of 12 m-width designed by forestry planners to isolate afforestation stands to control fires, also plays a relevant role for mammal diversity in afforested landscapes of Uruguay, by connecting patches of native vegetation.

1. Introduction

One of the main drivers of global biodiversity loss is human-driven land use and land cover change, which has resulted in habitat loss, fragmentation, and degradation at a very rapid rate (Graham et al., 2019; MEA, 2005; Newbold et al., 2016, 2015). The implementation of protected areas has been the main conservation instrument to halt biodiversity loss (Kareksela et al., 2013; Mace, 2014; Xavier da Silva et al., 2018), but it is insufficient to counteract the current and expected expansion and intensification of environmental alterations (Bowyer et al., 2019; Mace, 2014; UNEP-WCMC et al., 2018). In order to develop productive strategies compatible with conservation, focused on the prevention, reduction and mitigation of habitat loss and fragmentation, it is essential to evaluate the effects of productive activities on the different components and aspects of biodiversity (Brazeiro, 2015; Decarre, 2015; Fahrig, 2003; Fischer and Lindenmayer, 2007; Kshettry et al., 2020) and enhance landscape connectivity by maintaining corridors between patches of remaining unmodified areas (Resasco, 2019; Zeller et al., 2020).

Afforestation with exotic species for wood production or pulp is a productive activity in global expansion, which drives the transformation of important areas of natural, semi-natural or productive land (i.e., under other productive uses), in monospecific plantations (FAO, 2019). In the temperate region of South America (*sensu* Koppen classification), the conversion of natural grasslands into crops and monospecific tree plantations has reached outstanding levels, especially in the Río de la Plata Grasslands (RPG) region (-Baldi and Paruelo, 2008; Gautreau, 2014; Jobbágy et al., 2006; Leidinger et al., 2017). Uruguay, fully immersed in the RPG (Paruelo et al., 2007; Soriano, 1991), has experienced a strong expansion of grassland afforestation (*Eucalyptus* and *Pinus* genera); during the last 30 years, it went from less than 2,000 km^2 before the 1990 s, to more than 12,000 km^2 in 2019, covering 5.6% of the Uruguayan territory (DIEA-MGAP, 2019).

The effects of this activity on biodiversity have been focus of international debate, contrasting the idea that tree plantations are "green deserts" with no value as habitat for species (e.g. Bremer and Farley,

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2010; Fischer et al., 2014; Gonthier et al., 2014; Veldman et al., 2015), to the idea that under certain conditions these novel ecosystems can become valuable “habitats” (Brockerhoff et al., 2008; Crooks, 2002; Kennedy et al., 2013; Law et al., 2017; O’Callaghan et al., 2016). The afforestation-biodiversity relationship has been relatively well studied in forest-dominated landscapes (e.g. Basiron, 2007; Bauhus et al., 2010; Dormann et al., 2007; Felton et al., 2010; Hua et al., 2016; Lindenmayer et al., 2015, 2019; Pawson et al., 2008), but the evaluations are still few in grassland-dominated landscapes (Campos et al., 2018; Dotta and Verdade, 2011; Iezzi et al., 2020; Jobbágy et al., 2006; Lantschner, 2012; Veldman et al., 2015).

Mammals, and particularly medium and large-sized ones, have been scarcely studied (Iezzi et al., 2020; Law et al., 2017; Riffell et al., 2011) in grassland afforestation systems. But they play an important role in the ecosystems by representing most of the wildlife biomass (Redford, 1992), being the top predators and executing a top-down control over other vertebrates (Colman et al., 2015; Estes et al., 2011; Ripple et al., 2014) or playing an important role as seed dispersers (Howe, 1986; Vidal et al., 2013). In Uruguay, only two studies have quantitatively evaluated the afforestation-mammal relationship (Andrade-Núñez and Aide, 2010; Brazeiro et al., 2018), showing that the generalist species were dominant in tree plantations.

Thus, in this work we evaluate the local effect of the substitution of grasslands by eucalyptus plantations on the diversity of medium and large-sized mammal assemblage in Uruguay, focusing on two main questions: (1) What is the local effect (i.e., stand scale) of replacing grasslands by afforestation on species richness, composition, and intensity of habitat use? (2) How do different habitats and trophic specialization of mammal species correlate with use intensity of tree plantation?

2. Methods

2.1. Study areas

Uruguay, located in the southeast of South America (30°05′08″-34°58′27″S, 53°10′58″-58°26′01″W), has a continental area of 176,215 km^2. The climate is classified as Humid subtropical -or temperate *sensu* INUMET (INUMET, 2020), type “Cfa” *sensu* Köppen-Geiger- (Beck et al., 2018; Köppen and Geiger, 1926). The mean annual temperatures ranging between 16 °C at the SE and 20 °C at the NW and mean annual rainfall between 1100 mm.y^{-1} at the S and 1600 mm.y^{-1} at the NE (INUMET, 2020). Temperature is strongly seasonal with hot summers and cold winters, and precipitation is evenly distributed during the year, but strongly variable between years (INUMET, 2020). According to the official land-cover map of 2015, natural grasslands represent the dominant ecosystem (~60%) in the Uruguayan landscape, with native forest representing 4.8% and other native ecosystem (e.g., wetlands, shrublands) less than 1% (MVOTMA-DINOT, 2015). The most widespread productive activity is cattle breeding for meat and milk, mainly in grasslands (natural and semi-natural), but also in forests, savannas and some wetlands (DIEA-MGAP, 2019). Among anthropic covers, croplands (including artificial grasslands) represent 27.5% of the territory, afforestation 7.9% and urban and other artificial areas about 0.8% (MVOTMA, 2012).

This study was carried out in two of the main afforested regions of Uruguay, on the west and center of the country (Fig. 1, Figure S1); five landscapes afforested with *Eucalyptus dunnii* of 8–10 years (pre-harvest stage) were studied. The landscapes studied were dominated by natural habitats (grasslands, wetlands, forests, water courses) covering between 59 and 77% (mean: 64.8%, standard deviation: 7.7%), while forest plantations and agricultural crops had covers of 23–41% (mean: 35.5%, standard deviation: 7.7%). Firebreaks, i.e., the linear structures of

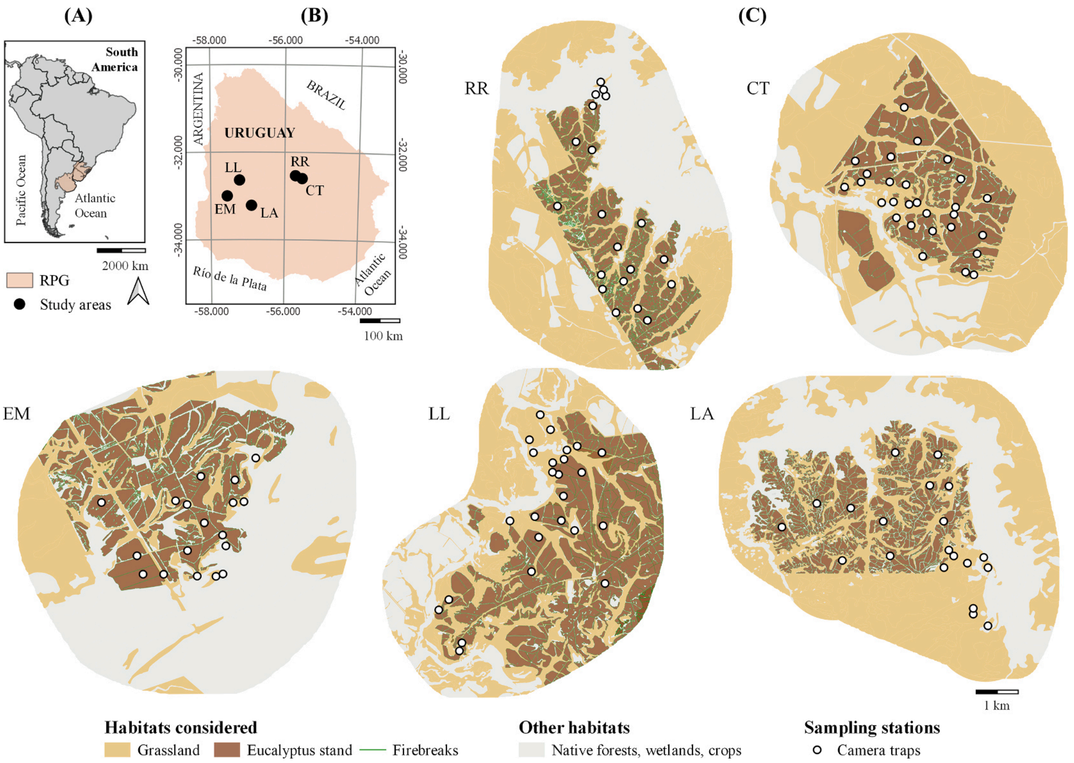

Fig. 1. Sampling stations in study areas: five grassland-dominated landscapes afforested with *Eucalyptus dunni* in Uruguay. (A) The extension of Río de la Plata Grasslands (RPG) in Uruguay and South America is shown in light red. (B) Location of the five study areas. Codes are as follow: EM: El Matorral, LL: Las Lilas, LA: Los Arroyos, RR: Rincón del Río, CT: Cueva del Tigre. (C) Land-covers considered at the studied landscapes: eucalyptus stands, firebreaks and grasslands. The sampling stations of camera traps are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

grasslands of 12 m-width (shrubs and trees are controlled) separating afforestation stands of maximum 50 ha, according to the Forestry Law of Uruguay, occupied about 5–10% of the forest plantation areas.

Afforestation management in all study areas does not involve thinning (the removal of a proportion of the trees at certain age to avoid growth competition) or pruning (cutting away dead or overgrown branches or stems to increase growth). The spacing between lines was 3 m and the spacing of trees within lines was 3 m too, with a tree density of 1,111 trees per hectare, with timber regimen (trees directly by seeding or from tree clones planted in each cycle, not by regrowth from the previous plantation cycle).

The Uruguayan assemblage of medium-large body size include 32 species, 26 natives and 6 exotics (González and Martínez-Lanfranco, 2010; Grattarola et al., 2016). In our study area, the regional pool of medium-large mammals is restricted to 21 species (18 native and 3 exotic), including the Orders Artiodactyla (2 native and 1 exotic), Carnivora (11 native), Cingulata (3 native species), Didelphiomorphia (1 native), Lagomorpha (1 exotic) and Rodentia (2 native). The list of potential species is shown in the Appendix I (Table S1).

2.2. Sampling design and mammal survey

The sampling design was established to be able to compare the different attributes of the medium and large-sized mammal assemblage between grasslands (i.e., natural environment, control) and eucalyptus stands (i.e., new environment that replaces grasslands). For this purpose, between 2015 and 2017 a total of 111 sampling points were surveyed, 52 sites in grasslands and 59 in eucalyptus plantations (Fig. 1). In these sites, the surveys were carried out using camera traps (Stealth Cam G42NG) -one per station-, which were established following a stratified random sampling design by habitat type at each study site (Fig. 1, Figure S1) considering: grasslands, eucalyptus stands and firebreaks. Firebreaks are uncultivated linear strips that are part of the planning strategy of eucalyptus stands; Some of them, besides working as blockers against potential fires, as their name implies, are used as internal roads (Minaverry, 2016). The camera traps remained active for 90 days in each sampling site. They were arranged with a minimum separation of 500 m, trying to reduce the probability of detecting the same individuals in different cameras (independence between stations) and at the same time optimizing the area to be covered. The mapping, selection, and placement of sampling points were performed using QGIS 2.14.15 (QGIS Development Team, 2018). More details about camera traps set up and installation are shown in the Supplementary Material (Appendix I).

2.3. Data processing

Exifpro image management software (Kowalski, 2013) was used for image processing, tagging species and extracting pictures metadata. The analysis was continued with the camtrapR package (Niedballa et al., 2020) in the statistical software R (R Core Team, 2020).

To avoid multiple counting of the same individual at a sampling station for a short period of time, all images of the same species taken over a period of one hour were considered as an independent event. When several individuals appeared together, the number of visits (or independent events) were considered as the number of visiting individuals. The one-hour span was considered adequate in similar camera trap studies for mid-large sized mammals (e.g. Decarre, 2015; Lantschner, 2012). Furthermore, to assess the selected separation among cameras, we checked that there were no records of the same specimens in nearby sampling stations within 2 h. Livestock species was not considered within species richness nor subsequent analyses.

2.4. Statistical analysis

2.4.1. Sampling completeness

To analyze the effectiveness of the surveys and completeness of the inventories, species accumulation curves were performed for both grassland and tree plantation habitats, using 999 iterations in R with the vegan package (Oksanen et al., 2019). As each habitat component had a different number of camera trap stations, we performed coverage-based rarefaction curves to estimate sampling completeness (Chao and Jost, 2012) in grasslands, firebreaks and eucalyptus stands. The analysis was performed with the R package iNEXT (Chao et al., 2014; Hsieh et al., 2020). More details on sampling completeness and diversity estimations are shown on the Appendix II of Supplementary Material.

2.4.2. Mammalian assemblage: Species richness, capture rate and composition

Using the complete set of photos in each study area, we obtained the number of observed species (species richness) and their respective capture or detection rate per each of the five sites. The capture rate (CR) was calculated as the number of independent events (records) over the sampling effort (camera-nights) multiplied by 100 (CR units hereafter: records/camera nights). The calculation of the CR is usually controversial. Following recommendations of Carbone et al. (2001) and Decarre (2015), we aimed at controlling for differential imperfect detection across sampling conditions through design (Banks-Leite et al., 2014) and assumed the observed responses in mammals species are not artifacts produced by unaccounted detectability. Considering this, the CR was used as an index of the intensity of habitat use.

In addition to the total species richness, we evaluated richness of native and exotic mammal species. Furthermore, we assessed richness of native species across environmental conditions with respect to habitat and trophic specialization. The first grouping considered habitat preferences, classifying species into three subgroups: (1) specialists of open environments (e.g., grasslands), (2) specialists of closed environments (e.g., riparian forest, hill forest) and (3) generalists (species adapted to ecotonal or intermediate and/or facultative environments in both closed and open covers). The second grouping of native species was according to trophic guilds: omnivores, carnivores, herbivores, and insectivores. The species segregation was carried out based on the specialized bibliography at the national level (González and Martínez-Lanfranco, 2010) and personal experience in the field.

2.4.3. Differences among habitats

Species richness and capture rate variability across treatments was assessed using Kruskal-Wallis H Test (also known as non-parametric ANOVA) (Quinn and Keough, 2002). We first tested the homogeneity of variance among treatments using the Fligner-Killeen's test, a non-parametric test which is very robust against departures from normality. There were no statistical differences in species richness ($H = 3.606$, $p = 0.642$) and overall capture rate ($H = 3.948$, $p = 0.513$) among the five sites. Therefore, we used a simple one-factor analysis to evaluate differences in richness and capture rate between grasslands, firebreaks, and eucalyptus plantations, pooling the complete dataset. When significant differences were found, post-hoc tests were performed using the Mann-Whitney test between each pair of groups, also called Wilcoxon's range test (Quinn and Keough, 2002). All analyzes were performed with the "stats" basic package from R software (R Core Team, 2020) and "cars" package (Fox and Weisberg, 2019).

Finally, we plotted species composition according to their mean capture rate and frequency of occurrence (incidence: sites with record) to classify them as occasional (species with capture rates higher than mean values, and lower incidence), dominant (capture rates and incidence both higher than mean values), rare (capture rates and incidence both lower than mean values), and frequent or constant (capture rates lower than mean values and incidence higher) using a modified Olmstead Tukey diagram (Sokal and Rohlf, 1969).

3. Results

3.1. Sampling completeness

We successfully recorded data in 111 sampling stations with an average sampling effort per station of 90 camera-nights (range: 87–105 camera nights), reaching a total effort of 9,043 camera-nights. Details are shown in Table 1.

The three samples for the different habitat components have almost identical sample coverage values (99.27%, 99.81% and 100% for firebreak, grassland and eucalyptus stand respectively), implying they are equally complete (see Appendix II), and the species accumulation curve reached saturation in the studied habitats (Figures S2). Therefore, the data can be directly compared according to Chao and Jost (2012) and allows making more robust inferences about the sampled mammalian assemblage (details on diversity estimations are shown in Appendix II, Table S2, Figure S3 and S4).

3.2. Mammalian assemblage

During systematic surveys we obtained around 2,000,000 pictures, from which 501 were considered independent records of wildlife species (Figure S5, Appendix III). Overall observed species richness was 14 species, with 11 being native and 3 exotic species (Table 2, Figure S6, Appendix III). Based on habitat preference, a single native species was identified as an open environment specialist (Table 2), the southern long-nosed armadillo (*Dasypus septemcinctus*). Three species were specialists in closed environments and seven species were classified as generalists. Regarding the trophic guilds, only one was herbivorous (*Hydrochoerus hydrochaeris*), two carnivores (*Galictis cuja* and *Leopardus geoffroyi*), three insectivores and five omnivores (Table 2).

All species groups were represented in all grasslands (Table 2). In eucalyptus stands, only habitat generalists, omnivores and insectivores were recorded; the other species groups were absent (Table 2). Finally, in firebreaks all groups were present except herbivores and those preferring open environments, represented by *H. hydrochaeris* and *D. septemcinctus* (Table 2).

3.3. Differences among habitats

The main significant differences occurred between the eucalyptus stands and all the other contrasting habitats: grasslands and firebreaks (Fig. 2, Appendix IV Table S3). There were no significant differences among grassland and firebreaks for any species group (Fig. 2, Appendix IV Table S3). The means overall richness and capture rate were also significantly higher in grasslands (Fig. 2, Appendix IV Table S3), almost twice in the case of the richness and threefold in the capture rate from eucalyptus stand (Fig. 2, "All"). The means richness and capture rates of the native species assemblage were also twice and threefold in grasslands compared to eucalyptus stands (Fig. 2, "Na"; Appendix IV Table S3). There were no differences in exotic species richness between habitats (Fig. 2, "Ex"; Appendix IV Table S3), but there was a higher capture rate on firebreaks, followed by grassland (Fig. 2, "Ex").

Table 1
Sampling effort on grassland, firebreak and eucalyptus stand per study area given in number of sampling stations (i.e., number of camera stations) and cameras-nights (between brackets). Study areas abbreviations are as follow, CT: Cueva del Tigre, EM: El Matorral, LL: Las Lilas, LA: Los Arroyos, RR: Rincón del Río.

Habitats	Sampling stations (cameras-nights) per study zone					
	CT	EM	LL	LA	RR	Total
Firebreak	5 (460)	3 (202)	2 (146)	4 (317)	2 (185)	16 (1310)
Eucalyptus stand	11 (996)	6 (429)	10 (913)	6 (448)	10 (799)	43 (3585)
Grassland	12 (1092)	9 (690)	13 (976)	10 (754)	8 (636)	52 (4148)

Table 2
Medium and large-sized mammals detected by camera traps in this study. Species are classified according to their habitat preference (Op: open habitats specialist, Cl: closed habitats specialist, Ge: generalist) and trophic guild (Her: herbivore, Car: carnivore, Ins: insectivore, Omn: omnivore) (González and Martínez-Lanfranco, 2010). The species mean capture rate and standard deviation by habitat (Grass: Grassland, EucS: Eucalyptus Stand, Fireb: Firebreak) is given. *: Exotic species.

Species (common name)	Habitat preference	Trophic guild	Mean CR (±SD)		
			Grass	EucS	FireB
*Axis axis** (Axis deer)	Ge	Her	1.09 (±0.22)	0.98 (±0.18)	0.87 (±0.12)
Cerdocyon thous (Crab-eating fox)	Cl	Omn	1.20 (±0.17)		1.02 (±0.49)
Conepatus chinga (Molina's hog-nosed skunk)	Ge	Omn	2.67 (±0.82)		0.54 (±0.13)
Dasypus septemcinctus (Southern long-nosed armadillo)	Op	Ins	2.25 (±0.27)		
Dasypus novemcinctus (Nine-banded armadillo)	Ge	Ins	3.99 (±0.76)	1.69 (±2.08)	4.38 (±0.47)
Didelphis albiventris (White-eared opossum)	Ge	Omn	1.17 ± (0.04)		
Euphractus sexcinctus (Six banded armadillo)	Ge	Ins	2.83 (±1.15)	0.85 (±0.23)	0.97 (±0.46)
Galictis cuja (Lesser grison)	Ge	Car	1.86 (±0.07)		
Hydrochoerus hydrochaeris (Capybara)	Ge	Her	1.40 (±0.08)		
Leopardus geoffroyi (Geoffroy's cat)	Cl	Car	1.37 (±0.15)		0.88 (±0.37)
*Lepus europaeus** (European hare)	Ge	He	1.14 (±0.91)	0.49 (±1.46)	2.73 (±0.18)
Lycalopex gymnocercus (Pampas fox)	Ge	Omn	4.89 (±1.62)	1.51 (±1.28)	1.86 (±0.22)
Procyon cancrivorus (Crab-eating raccoon)	Cl	Omn	1.14 (±1.10)		1.02 (±0.36)
*Sus scrofa** (Wild boar)	Ge	Omn	2.32 (±0.27)	2.69 (±0.31)	1.16 (±0.35)

Besides uncovered differences in species richness, grasslands, eucalyptus stands, and firebreaks showed different assemblage composition (Fig. 3). Fig. 3 shows the mammals assemblages observed in grasslands, eucalyptus stands, and firebreaks, plotting species according to their capture rates and incidence (station with records). Two dominant species were detected in grasslands, with high capture and incidence rates, *L. gymnocercus* and *D. novemcinctus* (Fig. 3a). Both species are generalists in terms of habitat preferences and about their trophic guilds, the first is omnivorous and the second is insectivorous. Four species are common in terms of incidence (*E. sexcinctus, C. chinga, C. thous, L. europaeus*), followed by four others with intermediate frequencies (*S. scrofa, A. axis, L. geoffroyi, P. cancrivorus*) (Fig. 3a). The remaining four species are relatively rare in capture rate and incidence (*G. cuja, H. hydrochaeris, D. septemcinctus, D. albiventris*) (Fig. 3a). In firebreaks (Fig. 3b), the two generalist species were also dominant, while the rest were occasionally

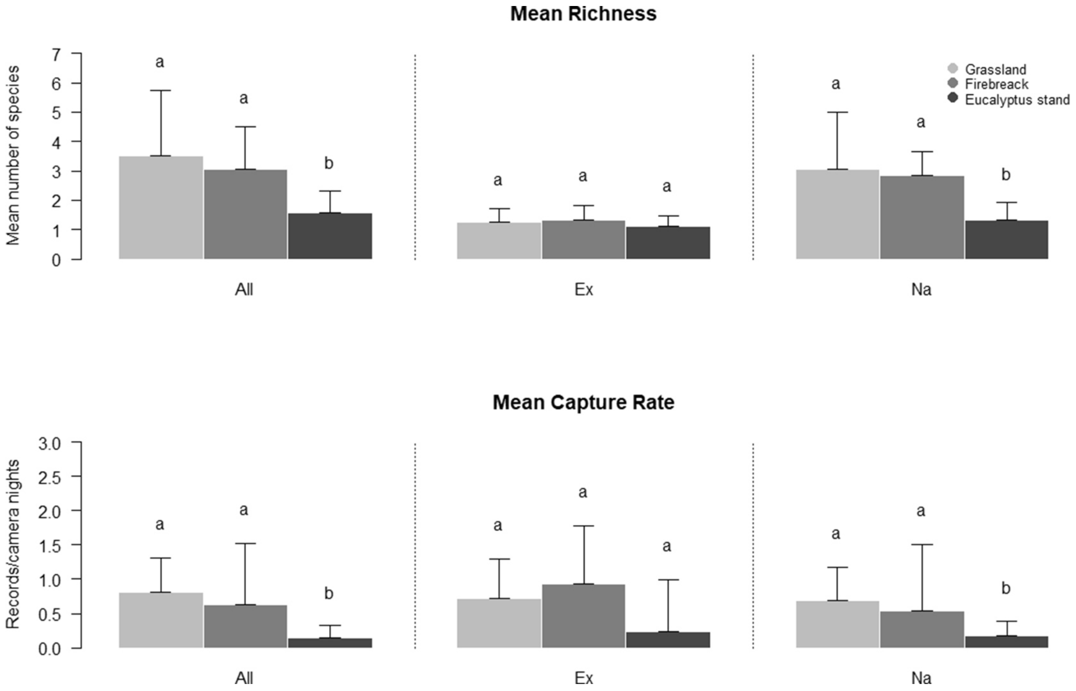

Fig. 2. Mean species richness (upper panel) and mean capture rate (lower panel) for grasslands, firebreak, and eucalyptus stand. Mean values and standard deviations (bars) are given. Different letters indicate significant differences between habitats; same letters mean no significant differences (*P*-values are shown on Table S3). All: All Species, Ex: Exotic, Na: Native.

recorded. Species categorized as rare in grasslands were not recorded in this habitat component, all the others were present. In the eucalyptus stands (Fig. 3c) the same two generalist species were also recorded as dominant, followed by *S. scrofa* as an occasional species and another three much rarer in terms of capture rate and incidence (*A. axis, E. sexcinctus, L. europaeus*).

4. Discussion

The main findings of our work, that includes the study of five landscapes during two years with 111 camara trap stations are the following: (1) The substitution of native grasslands by eucalyptus stands generate a reduction in species richness and captures rates, mainly by the loss of rare (i.e., low incidence and capture rate) and native specialist species. This reduction of native specialist causes plantation stands having a poor mammal assemblage, with half of the recorded species being exotic ones. (2) Afforestation is not a “green desert” in Uruguay, mainly due to the role of firebreaks, since 70% of the species were recorded on eucalyptus plantation when firebreaks are integrated. Firebreaks, i.e., the linear structures of grasslands of 12 m-width designed by forestry planners to isolate afforestation stands to control fires, also plays a relevant role for mammal diversity and connectivity in afforested landscapes of Uruguay.

4.1. Mammalian assemblage

The 14 registered species correspond to the 70% of the potential species for the study areas and around 50% of the medium and large-sized terrestrial mammals of Uruguay (González and Martínez-Lanfranco, 2010). The potential species that were absent on the surveys are rare and threatened (e.g., Puma -*Puma concolor*-, Maned wolf -*Chrysocyon brachyurus*-) or are difficult to detect given their ecology (e.g., Coypu -*Myocastor coypus*-, Pantanal cat -*Leopardus braccatus*-). All potential species that frequently use grassland were recorded in the afforestation landscapes, as seen in other open habitats of Uruguay regarding species composition (Cravino et al., *in prep*).

4.2. Differences among habitats

Our results show that the substitution of grasslands for eucalyptus plantations generates a negative impact at the local scale on the assemblage of medium and large-sized native mammals in the five study areas, reducing the cumulative species richness by 30% and mean capture rate by 54%, compared to grasslands, when considering stands and firebreaks as an adjacent combo. The mean values of richness and capture rate per camera-trap station were also higher in grasslands, almost twice in the case of the richness and threefold in the capture rate.

On the other hand, the evidence also shows that tree plantations (i.e., stands + firebreaks) are not “green deserts” (*sensu* Bremer and Farley, 2010) since 70% of the species were recorded on this new environment, meaning that most medium and large-sized mammals do not perceive these tree plantations as a barrier. This also shows that mammalian species are not equally affected by the replacement of grasslands by afforestation. According to our results, habitat and trophic preferences influence the species susceptibility to habitat change since specialist species are lost in the plantations. In contrast to our results, Iezzi et al. (2020) did not find differences between grasslands and pine plantations in northern Argentina, allowing them to conclude there are not substantial negative effects on the grassland mammal’s assemblage, despite the structural differences between these two environments. No species were exclusively photographed in tree plantations, same as in other similar studies (Andrade-Núñez and Aide, 2010; Iezzi et al., 2020; Timo et al., 2015).

4.3. Interspecific variability in the sensitivity of native species to afforestation

Generalist species were dominants, i.e., the most common and frequent both in grasslands and in afforestation, as was reported in previous studies (e.g. Andrade-Núñez and Aide, 2010; Iezzi et al., 2020). Among these species, *L. gymnocercus* and *D. novemcinctus* stand out. Given that generalist species are normally the ones that best adapt to new transformed environments (Andrade-Núñez and Aide, 2010; da

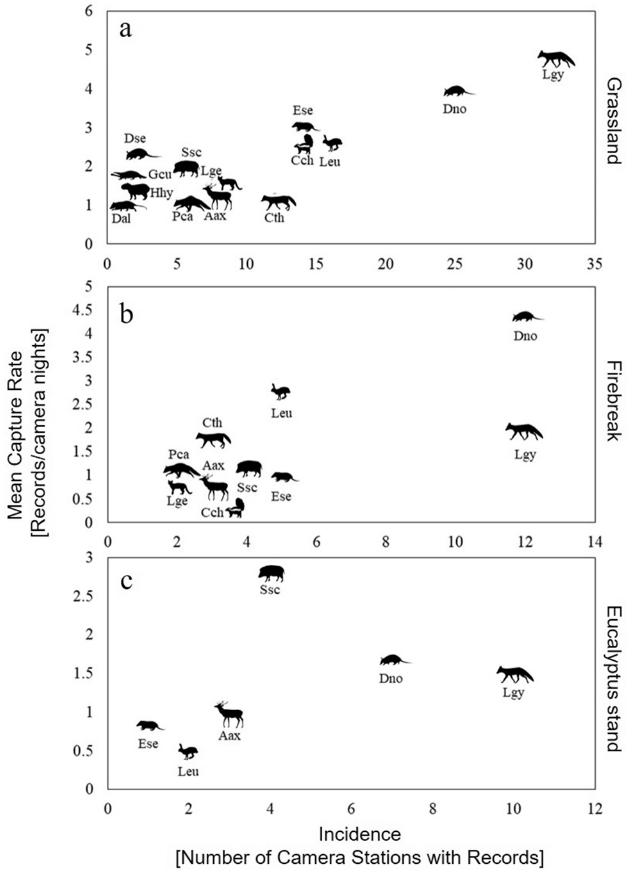

Fig. 3. Capture rate and incidence for all mammal species detected in the present study across grassland (a), firebreaks (b) and eucalyptus stand (c). Species codes: Aax: *Axis axis*, Cch: *Conepatus chinga*, Cth: *Cerdocyon thous*, Dal: *Didelphis albiventris*, Dno: *Dasypus novemcinctus*, Dse: *Dasypus septemcinctus*, Ese: *Euphractus sexcinctus*, Hhy: *Hydrochoerus hydrochaeris*, Gcu: *Galictis cuja*, Leu: *Lepus europaeus*, Lge: *Leopardus geoffroyi*, Lgy: *Lycalopex gymnocercus*, Pca: *Procyon cancrivorus*, Ssc: *Sus scrofa.* The silhouettes were vectorized from illustrations (De Angelo et al., 2017). Note the different scales in the y-axis and x-axis between plots.

Silva, 2001; Dotta and Verdade, 2011; Lyra-Jorge et al., 2008; Mosquera-Guerra et al., 2018; O'Callaghan et al., 2016; Silveira, 2005), our results were expected. This group of species was the only one observed inside the eucalyptus stands since no grassland nor forest specialist species were present in plantations.

Regarding the specialists of closed environments, although it could be assumed that eucalyptus plantations could end up favoring them given that they have a greater physiognomic similarity with native forests compared to grasslands, they presented higher records in grasslands. Inside afforestation they were recorded very occasionally, and only in firebreaks. Native forest sites were not included in this work, but it has been reported that mammal assemblages of plantations were more similar to those of grasslands than to those of forests, in terms of species richness and composition (Iezzi et al., 2020).

In our study areas, there is a single grassland specialist mammal, *D. septemcinctus*, which was only recorded in the remaining grasslands in the afforested landscape. No individuals of this species were found in eucalyptus stands or firebreaks. Although statistical analyzes could not be performed due to the low occurrences in the grasslands, our results suggest a high susceptibility of this species to the replacement of grasslands by afforestation. Logically, a higher susceptibility of habitat-specialist species to habitat loss and fragmentation would be expected. Giving support to this hypothesis, a review of changes in land-use and land-cover effects upon biodiversity found that habitat-specialists and narrow-ranging mammals have much-reduced probabilities of occurrence in modified habitats globally (e.g. Newbold et al., 2014). *D. septemcinctus* is considered a specialist in both diet and habitat preferences (Abba et al., 2015, 2011), thus it is likely more sensitive to human perturbation than other armadillos, such as *D. novemcinctus*. Our results provide new evidence supporting this hypothesis, agreeing with previous studies showing higher activities of *D. septemcinctus* in natural and less human-impacted habitats (i.e., grasslands) (Abba et al., 2016; Andrade-Núñez and Aide, 2010; Bilenca et al., 2017). Afforestation could be negatively affecting this species in two ways, through reducing and fragmenting its principal habitat, but also by their main food source, ants. Ants control is common forestry management in Uruguay, principally during the first two years of the productive cycle and before harvest, by managing leaf-cutter ants (Montes del Plata, 2019). Given its double vulnerability to forestry activity, the conservation of this specialist armadillo should be of main concern for responsible forestry management in Uruguayan grasslands.

Regarding trophic guilds of native species, insectivores were present in both grassland and afforestation (i.e., stands + firebreaks). *E. sexcinctus* and *D. novemcinctus* were frequent in afforestation, so this type of diet could be being favored in adult eucalyptus plantations, since both ants and termites are usually abundant -not as much as in native forests- (Junqueira et al., 2008; Martello et al., 2018; Suguituru et al., 2011). A high number of burrows of both species were also observed in plantations, especially towards the edges and in firebreaks (AC personal observation), where the sandy soil could also favor the construction of burrows. Another guild very well represented in the afforestation were the omnivores, whose species are normally characterized by being trophic generalists and opportunists (Andrade-Núñez and Aide, 2010; da Silva, 2001; Dotta and Verdade, 2011; Law et al., 2017; Lyra-Jorge et al., 2008). One of the known consequences of dense plantations, such as those studied here, is that the herbaceous strata and understory vegetation practically disappears in advanced stages of the cycle (Brazeiro et al., 2020; Six et al., 2014). Several studies have shown that grassland afforestation with lower tree densities have favorable effects on mammals (Converse et al., 2006; Lantschner, 2012; Suzuki and Hayes, 2003). Plantation thinning, a common management practice, could create a more permeable habitat for some species by allowing the development of understory vegetation, providing greater food availability and cover (Iezzi et al., 2020; Lantschner, 2012). The two carnivores, *L. geoffroyi* and *G. cuja*, showed higher capture rate in grasslands, but they were only occasionally registered in firebreaks too, while not on tree stands. This pattern was also observed in other regions (Decarre, 2015; Lantschner, 2012), suggesting the potential role of firebreaks as corridors and connectors between native vegetation patches on either side of them.

4.4. Exotic species assemblage

At a global level several works have affirmed or put on the table that the substitution of grassland-matrix by afforestation could have positive effects on exotic species, that normally are generalists and more tolerant to modified ecosystems (Barnett et al., 1977; Kennedy et al., 2013; Law et al., 2017). In Uruguay, it has been suggested that the same could happen, to explain the expansion of *Sus scrofa* for example (Andrade-Núñez and Aide, 2010; Lombardi et al., 2007), but it has not been evaluated yet.

In the present work, no significant differences were observed in the richness or capture rate of exotic mammals between grasslands and afforestation, but half of the species recorded in afforestation were exotic since the species lost were all native.

4.5. Firebreaks as potential habitat corridors

When the area of a certain natural habitat decreases, species richness, population abundance and also the genetic exchange within regional populations, can be reduced accordingly (Moreno and Guerrero-Jimenez, 2019). Biological corridors are one of the main strategies to promote the biodiversity conservation in fragmented landscapes, increasing connectivity between potential remaining favorable patches (e.g. González-Maya et al., 2013; Moreno and Guerrero-Jimenez, 2019).

The fact that the two carnivores have been recorded in firebreaks, is an indicator of the role that this plantation component (i.e., walkways with herbaceous vegetation free of trees 12 m wide, between eucalyptus stands) could have as corridors and connectors between native vegetation patches. It has already been demonstrated in various studies that mammals tend to use open environments, such as trails or roads, to circulate more efficiently through more closed landscapes (James and Stuart-Smith, 2000; Lantschner, 2012). In our region, there are some antecedents on the use of firebreaks by mammals in afforested landscapes, like in Argentina (Decarre, 2015; Lantschner, 2012), Brazil (da Silva, 2001; Silveira, 2005; Timo et al., 2015) and Chile (McFadden and Dirzo, 2018).

4.6. Methodological caveats

The sampling method used, despite not being designed for a particular species, is biased to species that make use of the ground, low strata, and understory , so those species with arboreal or semi-aquatic habits may had very low records or were not directly detected, according to expectations (Bowler et al., 2017). However, this sampling bias would not be relevant in our specific study, focused on grasslands mammals, of medium-large size.

Imperfect detection is a source of uncertainty when it was not controlled by detectability or environmental proxy variables of it, beyond the probability of being present or not, in addition to body sizes and species habits. Considering this, tall grasslands may have lower detection ranges due to high vegetation cover, compared to sparser stands and firebreaks. Therefore, the observed differences in mammalian assemblages, mainly in capture rates, between grassland and afforestation could be greater, but not less than those found in the present study.

5. Conclusions

5.1. Recommendations for conservation

We found 11 native mammal species from medium to large body size in the five study areas, four of them, all specialists, were absent in afforestation (i.e., stands + firebreaks). Among these absences, the most worrying is the one of *D. septemcinctus.* This is a specialist armadillo, both in diet (ant-feeding) and habitat preference (grassland) (Abba et al., 2015, 2011), distributed throughout the RPG region (Feijó et al., 2018). Understanding its ecological requirements to reach minimum viable populations would be crucial for the conservation of this armadillo in these afforested landscapes, originally dominated by grasslands. Maintaining some large patches of natural grassland, connected by a net of firebreaks, could be an interesting conservationist measure to probe.

The firebreaks could be functioning as linear corridors within the exotic plantations that communicate the different patches of remaining native vegetation, not only grasslands, but also various types of forests. The context of the landscape and the surrounding native remnants are crucial for the maintenance of biodiversity. Firebreaks could be a key link for the conservation of species and connectivity in afforested grassland landscapes.

CRediT authorship contribution statement

Alexandra Cravino: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition. **Alejandro Brazeiro:** Conceptualization, Formal analysis, Investigation, Resources, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.118937.

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Supplementary Material for

Grassland afforestation in South America: local scale impacts of *Eucalyptus* plantations on Uruguayan mammals

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This file includes Appendix I-IV, Table S1 and S2, Figures S1-S6

Appendix I – Study Area and Methods Details

Study area

Three habitat components were considered in this work: grassland, firebreak, and *Eucalyptus* stand (Figure S1). All of them were sampled in five study areas.

Figure S1. Illustrative photographs of the habitat components taken from a drone by one of the authors from one of the study areas (LA: Los Arroyos).

Mammal species

The regional pool of medium-large mammals in the study areas is restricted to 21 species from 6 Orders and 13 Families. The complete list of potential species is shown in Table S1.

Table S1. List of potential mammal species from the study areas.

Order	Family	Scientific name	English common name	Native (N) / Exotic (E)	Recorded
Artiodactyla	Cervidae	*Axis axis*	Axis Deer	E	X
Artiodactyla	Cervidae	*Mazama gouazoubira*	Gray Brocket	N	
Artiodactyla	Suidae	*Sus scrofa*	Wild Boar	E	X
Carnivora	Canidae	*Cerdocyon thous*	Crab-eating Fox	N	X
Carnivora	Canidae	*Chrysocyon brachyurus*	Maned Wolf	N	
Carnivora	Canidae	*Lycalopex gymnocercus*	Pampas fox	N	X
Carnivora	Felidae	*Leopardus braccatus*	Pampas Cat	N	
Carnivora	Felidae	*Leopardus geoffroyi*	Geoffroy's Cat	N	X
Carnivora	Felidae	*Leopardus wiedii*	Margay	N	
Carnivora	Felidae	*Puma concolor*	Puma	N	
Carnivora	Mephitidae	*Conepatus chinga*	Molina's Hog-nosed Skunk	N	X
Carnivora	Mustelidae	*Galictis cuja*	Lesser Grison	N	X
Carnivora	Mustelidae	*Lontra longicaudis*	Neotropical Otter	N	
Carnivora	Procyonidae	*Procyon cancrivorus*	Crab-eating Raccoon	N	X
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded Armadillo	N	X
Cingulata	Dasypodidae	*Dasypus septemcinctus*	Southern Long-Nosed Armadillo	N	X
Cingulata	Euphractidae	*Euphractus sexcinctus*	Yellow Armadillo	N	X
Didelphiomorphia	Didelphidae	*Didelphis albiventris*	White-eared Opossum	N	X
Lagomorpha	Leporidae	*Lepus europaeus*	European Hare	E	X
Rodentia	Hydrochoerinae	*Hydrochoerus hydrochaeris*	Capybara	N	X
Rodentia	Myocastoridae	*Myocastor coypus*	Coypu	N	

Camera trap set up

The camera traps were active 24 hours a day throughout the sampling period and were programmed to take three 10-megapixel images upon activation by movement and temperature differences, with a high sensitivity mode and a subsequent 15-second latency. The camera model features a trigger speed of 0.5 seconds. Cameras were installed in trees or poles, facing South or North, to avoid false triggers due to direct sunlight exposure. Baits were not used, and adjacent vegetation that could activate or cover the cameras was removed to optimize detection and facilitate species recognition. The placement height was between 50 and 70cm, according to the average height of potential species, to reduce variations in detectability by body size and /or camera capture angle (Meek et al., 2016). The maximum detection distance was estimated at 3 meters from the placement site.

They were arranged with a minimum separation of 500 m, trying to reduce the probability of detecting the same individuals in different cameras (independence between stations) while optimizing the area to be covered. The 500 m distance was defined based on the minimum home range of two common Uruguayan species, the Pampas fox *Lycalopex gymnocercus* and the Crab-eating fox *Cerdocyon thous* (Di Bitetti et al., 2009; Luengos Vidal et al., 2012; Macfadem Juarez & Marinho-Filho, 2002; Maffei & Taber, 2003). These species were selected because their minimal home range includes the species with smaller areas of action.

Appendix II – Sampling completeness

The species accumulation curve reached saturation in the studied habitats: grassland, firebreak, and *Eucalyptus* stand. Figure S2 shows the species accumulation curve with the sampling stations as sampling effort measurement, considering that when the sampling unit is not an individual but a camera trap, these units, not the individual organisms, are sampled randomly and independently.

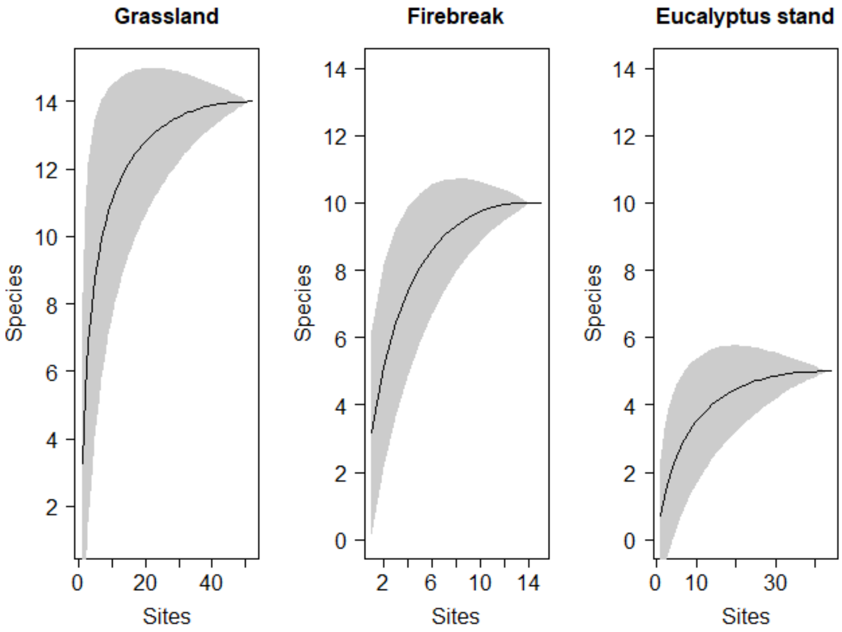

Figure S2. Species accumulation curves with 95% confidence intervals in relation to all sampled stations (Sites) in grassland, firebreaks, and *Eucalyptus* stands.

The three surveys for the different habitat components have almost identical sample coverage values (99.27%, 99.81%, and 100% for firebreak, grassland, and *Eucalyptus* stand respectively), implying they are equally complete to Chao and Jost (2012).

Considering that, besides the analysis of differences between habitat types, we estimated mammals true diversity per habitat using incidence data (Hill, 1973) with Hill numbers (D_q) considering the effective number of species and q parameters that consider sensibilities to species abundance (Chao et al., 2014; Jost, 2007). Diversity of order 0 (D_0) represents species richness, considering species based on their presence/absence, without considering their relative abundance, and therefore sensitive to rare species in the sample (Chao et al., 2014). Diversity of order 1 (D_1, exponential of Shannon diversity) weights the species according to their relative abundance, mostly reflecting species with low or medium abundance (common or typical species) (Chao et al., 2014). And the second-order diversity (D_2, inverse of the Simpson index) reflects the diversity of the species with high relative abundance, the dominant species (Chao et al., 2014). All values are shown in Table S1.

Table S1. Observed values and diversity estimations by Hill numbers D_0, D_1, and D_2.

	Sample coverage (%)	Diversity	Observed value	Estimated value	Standard error
Grassland	99.81%	D_0	14.00	14.50	1.32
		D_1	6.97	7.01	0.29
		D_2	5.14	5.18	0.27
Firebreak	99.27%	D_0	10.00	10.50	1.31
		D_1	5.17	5.37	0.50
		D_2	3.53	3.60	0.42
Eucalyptus stand	100%	D_0	5.00	5.00	0.40
		D_1	3.69	3.82	0.28
		D_2	3.25	3.38	0.28

Species richness among grassland and *Eucalyptus* stand was significantly different (none of the confidence intervals intersect); between grassland and firebreak, confidence intervals intersect at large sample sizes (left panel Figure S3, q=0). Considering D_1, grassland is the most diverse habitat component of common species, followed by firebreak and *Eucalyptus* stand, with no overlapping confidence intervals (middle panel Figure S3, q=1). D2 is higher for grassland as well, indicating a higher number of dominant species (middle panel Figure S3, q=2). *Eucalyptus* stand had a poorer but more even mammal assemblage (Figure S4), with species with a smaller frequency of appearance. The slopes of the curves in Figure S4 reflect the unevenness of species records. The more uneven the distribution of species records, the more steeply the curve declines (Chao et al., 2014). The same could be seen by the coefficient D_2/D_0: 0.68 for *Eucalyptus* stand, 0.36 for grassland, and 0.34 for firebreaks.

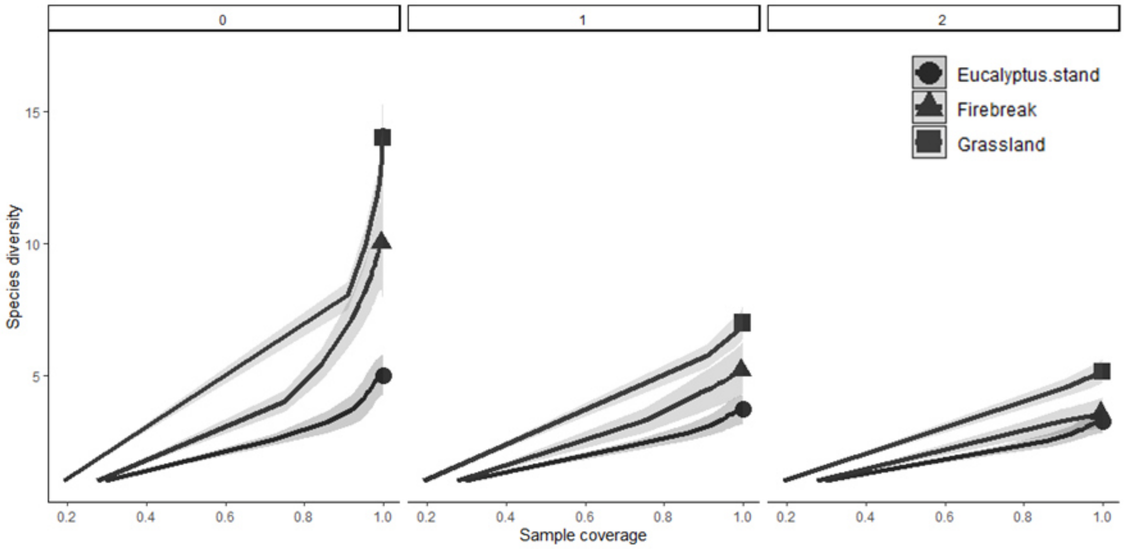

Figure S3. Coverage-based diversity accumulation curve with 95% confidence intervals (gray shade), which plots the expected diversity D_q as a function of expected coverage with $q = 0, 1,$ and 2 for “Grassland,” “Firebreak”, and “*Eucalyptus* stand”.

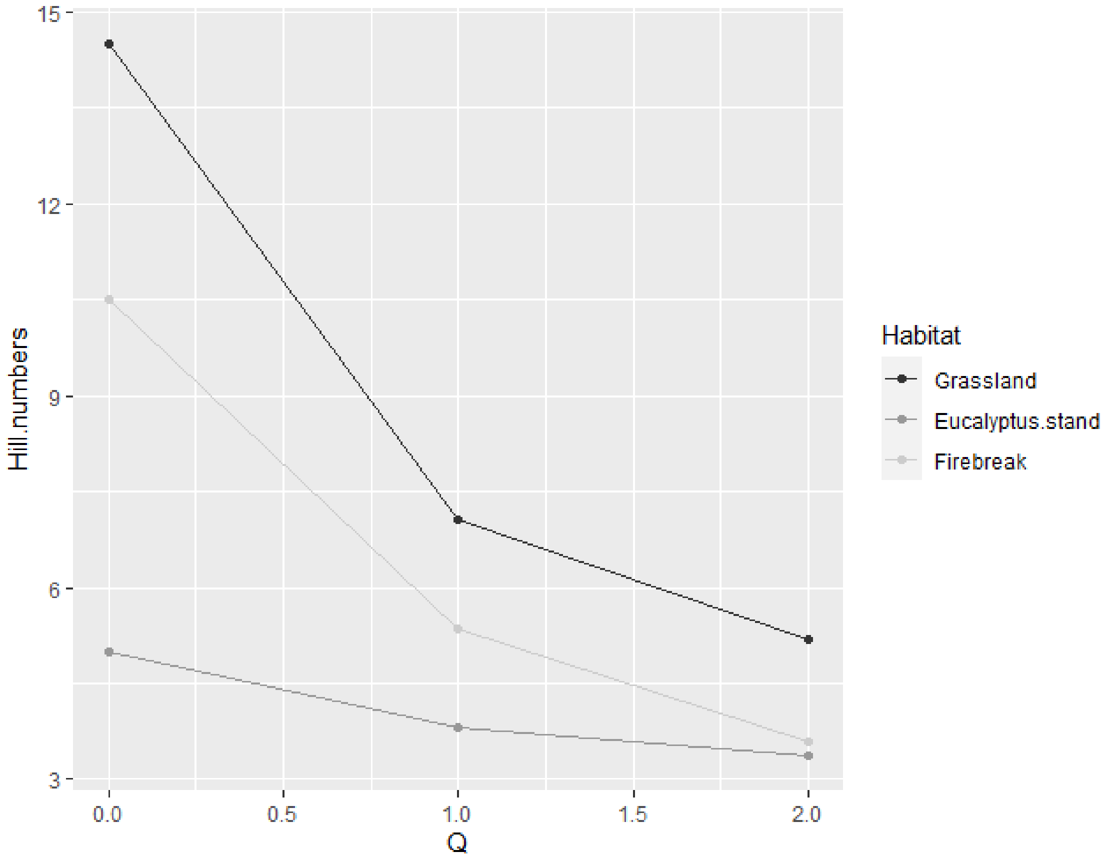

Figure S4. A diversity profile curve, showing Hill numbers D_q, with q = 0, 1, 2.

Appendix III – Mammal assemblage

During surveys, 14 mammal species were recorded with the camera traps. Examples of photographs of different species captured are shown in Figure S5.

Figure S5. Example of species recorded on camera traps. a) *Didelphis albiventris*, b) *Galictis cuja*, c) *Hydrochoerus hydrochaeris*, d) *Lycalopex gymnocercus*, e) *Axis axis*, f) *Sus scrofa.*

The cumulative species richness -cumulated number of species over sampling units- at the habitat level was higher in grasslands, with 14 total species compared with ten species recorded on firebreaks stations and five on *Eucalyptus* stands (Figure S6). The mean richness -mean number of species recorded over sampling units- was almost equal for firebreaks and grassland, with 3.32 (±0.35 s.e. -standard error-) and 3.20 (±0.37 s.e.) mean richness, respectively, while *Eucalyptus* stand reached 0.65 (±0.12 s.e.) in average (Figure S6).

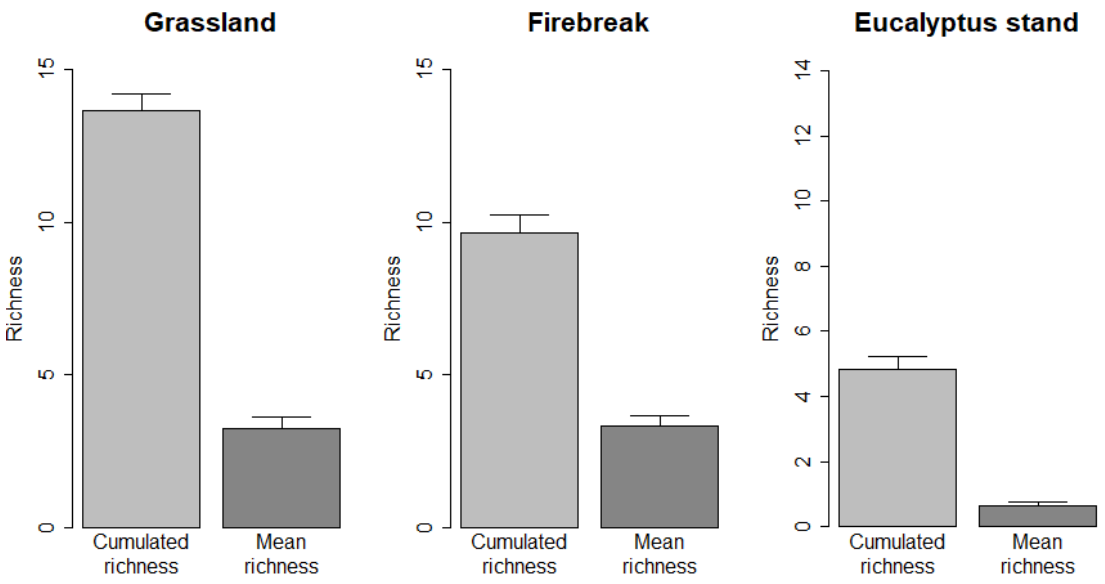

Figure S6. Cumulative and mean species richness for grassland, firebreak, and *Eucalyptus* stand. Bars represent the upper 95% confidence intervals estimated by bootstrap.

Appendix IV – Differences among habitats

We considered all species, native and exotic species, for our response variables: species richness -number of observed species- and capture rate -number of independent events (records) over the sampling effort-. Species richness and capture rate variability across treatments (grassland, firebreak, and *Eucalyptus* stand) were assessed using Kruskal-Wallis H Test (also known as non-parametric ANOVA). Significance means that at least one population median of one group is different from the population median of at least one other group. The test does not identify where this difference occurs or for how many pairs of groups; for analyzing the specific sample pairs, pairwise Mann–Whitney tests were used. The results of this pairs comparison are shown in Table S3.

Table S3. *P*-values from habitats pairwise contrasts. Significant differences are shown in bold.

Habitat pairwise contrasts	**Mann-Whitney Test *P*-values**					
	All species		**Exotic species**		**Native species**	
	Richness	**Capture rate**	**Richness**	**Capture rate**	**Richness**	**Capture rate**
Grassland-Firebreak	0.424	0.888	0.550	0.430	0.294	0.947
Grassland-*Eucalyptus* stand	**$9.0e^{-5}$**	**$1.1e^{-4}$**	0.320	0.300	**$1.8e^{-4}$**	**$1.4e^{-4}$**
Eucalyptus stand-Firebreak	**0.003**	**0.001**	0.270	0.210	**0.012**	**0.014**

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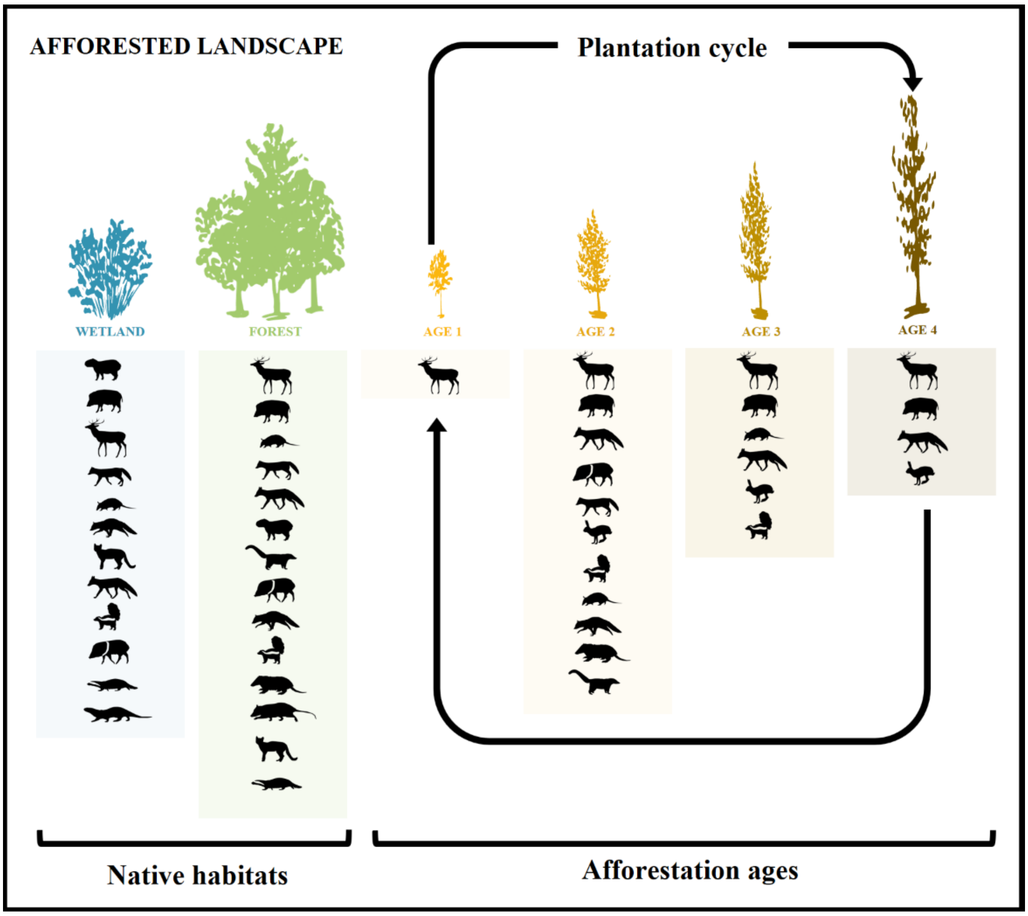
Estructura comunitaria de mamíferos de mediano y gran porte a lo largo de un ciclo de forestación sobre pastizal en Uruguay



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Community structure of medium-large mammals across a tree plantation cycle in natural grasslands of Uruguay

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Species turnover

ABSTRACT

In temperate South America, the conversion of natural grasslands into crops and exotic tree plantations, such as with *Eucalyptus* sp., has reached outstanding levels, especially in the Río de la Plata Grasslands. The cycle of *Eucalyptus* plantations for pulp production is a very dynamic phenomenon; however, most of the studies on the impacts on biodiversity have been static and focused on the mature stage of the plantation. We studied the mammal assemblage in a grassland afforestation landscape of Uruguay to address how mammals respond to habitat complexity variation across the plantation cycle and landscape characteristics. We installed 26 camera traps for two years in four different age stages of *Eucalyptus* plantations and native habitats to assess mammals' richness, composition, and intensity of habitat use. We registered 16 mammal species, 13 native and three exotics, with a sampling effort of 19,136 camera-nights. Of these species, 11 were found in the *Eucalyptus* plantations but with significant variability during the production cycle. Only one species was recorded at the beginning (0–2 years) of the cycle and four species at the end (8–10 years). But at intermediate ages (2–4 years), when vegetation complexity resembles a native forest structure, species richness was maximum (11 species) in the plantations and relatively close to forest richness (14 species). Species composition was also determined by habitat structure, but it was further modulated by landscape features, particularly the proximity to native forests and landscape heterogeneity. Our results demonstrated that asynchronous plantations promote spatial heterogeneity that favors mammal diversity in afforested landscapes, but for grassland mammals, additional conservation management measures are needed.

1. Introduction

Human-driven land use and land cover transformation are leading drivers of biodiversity change worldwide (Graham et al., 2019; MEA 2005; Newbold et al., 2016, 2015). Tree plantations with exotic species for wood production or cellulose are productive activities in global expansion, which drives the transformation of areas of natural, semi-natural, or productive land (i.e., under other productive uses) into monospecific plantations (FAO, 2019). In temperate South America, the conversion of natural grasslands into crops and tree plantations (i.e., afforestation) has reached outstanding levels, especially in the Río de la Plata Grasslands (RPG) (Baldi and Paruelo, 2008; Gautreau, 2014; Gorosábel et al., 2020; Jobbágy et al., 2006; Leidinger et al., 2017; Veldman et al., 2015). Uruguay, fully immersed within the RPG (Paruelo et al., 2007; Soriano, 1991), has experienced a strong expansion of grassland afforestation (*Eucalyptus* and *Pinus*) during the last 30 years, going from <2,000 km^2 before the 1990s, to >12,000 km^2 in 2019, covering 5.6 % of the Uruguayan territory (DIEA-MGAP, 2019).

The effects of afforestation on biodiversity have been a focus of international debate, contrasting the idea that tree plantations are "green deserts" with negligible importance for native species (e.g. Bremer and Farley, 2010; Fischer et al., 2014; Gonthier et al., 2014; Veldman et al., 2015), to the idea that, under certain environmental and management conditions, these novel ecosystems can become suitable habitats (Brockerhoff et al., 2008; Crooks, 2002; Kennedy et al., 2013; Law et al., 2017; O'Callaghan et al., 2016), being even less impactful than other alternative land uses that replace the native vegetation (i.e., agricultural crops) (Ferreira et al., 2018). Despite sharp changes in environmental conditions, such as in vegetation structure, along the productive cycle (Cooper, 1960; Santoandré et al., 2021), most research on the effects of afforestation focuses on the mature stages of the plantation cycle, whereas the early stages have received comparatively little attention

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(Iezzi et al., 2020; Pairo et al., 2020; Timo et al., 2015).

The plantation cycle starts with the land and site preparation, tree plantation (typically fast-growing clones), with weed and ant control during the first one to two years (Gabrielle et al., 2013; Montes del Plata, 2019). During this first stage, which is often excluded from cattle grazing, the plantation area assumes a bushy structure, followed by a forest structure with higher complexity due to low steam cover and understory. As the canopy begins to close, less sunlight reaches the floor. These changes in environmental conditions influence the understory and ground vegetation, evolving into a homogeneous forest with high, closed canopies with almost no understory vegetation. Clearcutting occurs at the end of 8–10 years when achieving maturity to harvest for cellulose production (Tomé et al., 2021; Turnbull, 1999; Wagner et al., 2006). Therefore, besides being symmetrically placed, these planted monospecific forests present an important temporal and structural heterogeneity that may affect the habitat quality for wildlife, influencing species occurrence and habitat use patterns (Dotta and Verdade, 2011; Iezzi et al., 2020; Timo et al., 2015).

Forest stand dynamics are defined as the structural changes in natural, semi-natural, or planted forests through time (Cannell and Last, 1976; Oliver and Larson, 1996). These tree stand variations through time generate a shifting landscape mosaic (Bormann and Likens, 1979) that could imply spatial and temporal modifications of habitats, affecting species diversity (Riva and Nielsen, 2020; Tscharntke et al., 2012). It remains key to evaluate how this landscape heterogeneity influences biodiversity patterns.

We studied the *Eucalyptus* plantation stand ages and native habitats on Uruguayan grasslands to assess how tree stands structural, and landscape variations through the cycle affected the medium-large mammal community at local and landscape scales. The study focused on two main questions: (1) How does the complexity of vegetation structure across plantation ages affect the medium-large mammal assemblage? (2) How do landscape composition and configuration under afforestation regimens modulate medium-large mammal assemblage? So firstly, given that vegetation structure and complexity are usually correlated to niche diversity and resource availability (e.g., LaRue et al., 2019; Turnbull et al., 2016), we hypothesized that medium-large mammal assemblage structure would vary according to vegetation changes through the plantation cycle, reaching the highest diversity at the highest vegetation complexity stages. Secondly, since the afforestation process reduces natural habitat availability at the landscape level (e.g., Iezzi et al., 2021; Veldman et al., 2015), we hypothesized that landscape homogeneity would reduce medium-large mammal diversity.

2. Methods

2.1. Study area

Uruguay, located in the southeast of South America (30°05′08″-34°58′27″ S, 53°10′58″-58°26′01″ W), has a continental area of 176,215 km2. The climate is classified as Humid subtropical or temperate (INUMET, 2020), type "Cfa" *sensu* Köppen-Geiger- (Beck et al., 2018; Köppen and Geiger, 1926). According to the official land-cover map of 2015, natural grasslands represent the dominant

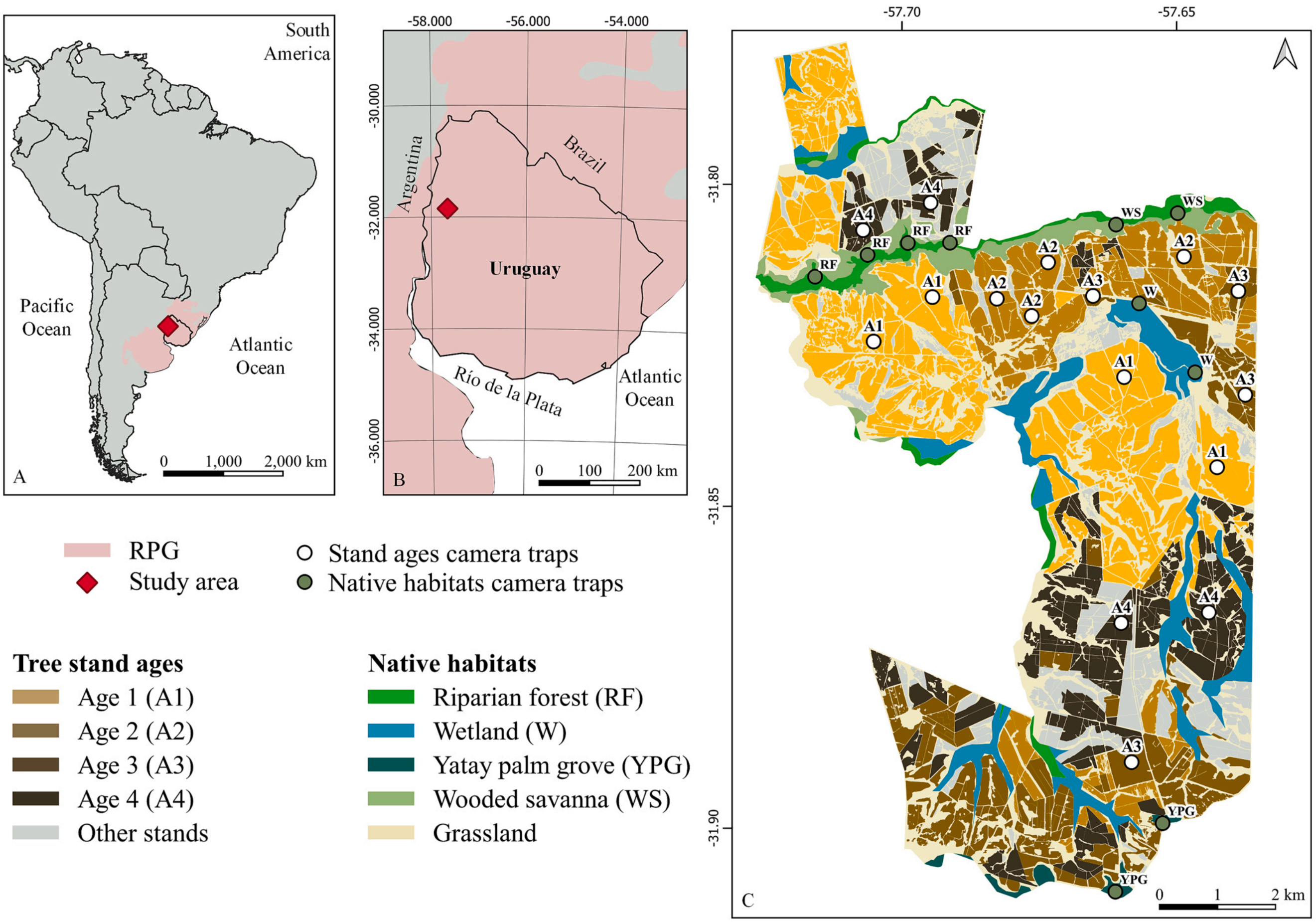

Fig. 1. Sampling stations in the grassland-dominated landscapes afforested with *Eucalyptus dunni* in Uruguay. (A) The extension of Río de la Plata Grasslands (RPG) in Uruguay and South America is shown in light red. (B) Location of the study area (Santo Domingo). (C) Stand ages (Ages 1 to 4) and natural habitats (Yatay palm grove, wooded savanna, wetland, riparian forest) are considered in the studied landscape. The sampling stations of camera traps are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ecosystem (~60 %) in the Uruguayan landscape, with native forests representing 4.8 % and other native ecosystems (e.g., wetlands, shrublands) <1 % (MVOTMA-DINOT, 2015). The most widespread productive activity is cattle ranching for meat and dairy, mainly in grasslands (natural and semi-natural) but permeates into forests, savannas, and wetlands (DIEA-MGAP, 2019). Among anthropic covers, croplands (including artificial grasslands) represent 27.5 % of the territory, *Eucalyptus* and *Pinus* afforestation 7.9 %, and urban and other artificial areas about 0.8 % (MVOTMA, 2012).

This study was carried out in one of the main afforested regions of Uruguay, in the northwest of the country (Fig. 1). A landscape afforested with *Eucalyptus dunnii* of different ages (from just planted to mature trees) was studied. It was dominated by plantations, covering 71.4 % of the area, while natural habitats (wetlands, forests, watercourses) covered 28.6 % (Supplementary Material: Appendix I, Figure S1, and S2).

Planted stands were composed of one tree species (i.e., *E. dunnii*), and had uniform tree spacing. Afforestation management did not involve thinning (the removal of a proportion of the trees at a certain age to avoid growth competition) or pruning (cutting away dead or overgrown branches or stems from increasing growth). The spacing between lines and within lines was 3 m, reaching a tree density of 1,111 trees per hectare, with timber regimen (trees directly planted by seeding or from tree clones planted in each cycle, not by regrowth from the previous plantation cycle). Wet or humid grasslands were found within uncultivated lowland areas throughout the landscape (Fig. 1). A high herbaceous cover characterized these wetlands. Native forests were mostly confined to riparian areas along rivers and streams (riparian forests) with close-by wooded savannas (Fig. 1). Yatay palm groves, characterized by a high cover of different palm tree sizes, were also found nearby southern tree plantations (Fig. 1).

The Uruguayan assemblage of medium-large mammals includes 32 species, 26 natives, and six exotics (González and Martínez-Lanfranco, 2010; González et al., 2021). In our study area, the regional pool of medium-large mammals is restricted to 23 species (20 natives and three exotics), including the Orders Artiodactyla (two natives and two exotics), Carnivora (12 natives), Cingulata (three native species), Didelphiomorphia (one native), Lagomorpha (one exotic) and Rodentia (two natives). The list of potential species is shown in Supplementary Material (Appendix I, Table S2).

2.2. Sampling design and mammal survey

The sampling design was established to compare the different attributes of medium to large-sized mammal assemblage between *Eucalyptus* stand age classes and native habitats. For this purpose, between September 2018 and September 2020, a total of 26 sampling points were surveyed continuously for 736 days (Fig. 1). In these sites, the surveys were carried out using camera traps (Stealth Cam G42NG) -one per station- distributed following a stratified random sampling design (Fig. 1), covering *Eucalyptus* plantations of different ages and native habitat types. Besides those 26 sampling points, in other 6 locations, camera traps were stolen.

Four categories of *Eucalyptus* tree plantations -hereafter tree plantations- were selected to represent the chronosequence associated with the commercial cycle focused on pulp production: stands from zero up to two years (hereafter, Age 1), from two up to four years (hereafter, Age 2), from four up to seven years (hereafter, Age 3), and from seven up to ten years (hereafter, Age 4). The two native habitats sampled correspond to native forests, including different physiognomic types (riparian forest, wooded savanna, and Yatay palm grove) and wet grasslands (hereafter, wetlands). The distribution of the 26 sampling stations among strata was as follows: 16 for tree plantations (four per age category), eight for native forests, and two for wetlands (Fig. 1). Camera traps were arranged with a separation of 1 km (among stand ages: mean = 1.25 km, min = 0.98 km, max = 7.45 km; among native habitats: mean = 1.06 km, min = 0.96 km, max = 11.81 km; overall distances: mean = 1.13 km, min = 0.98 km, max = 12.32 km), trying to reduce the probability of detecting the same individuals in different cameras (i.e., independence between stations) and at the same time optimizing the stands area to be covered. Stations were not autocorrelated (confirmed with Moran's Index, p-value > 0.05). The mapping, selection, and placement of sampling points were performed using QGIS 2.14.15 (QGIS Development Team, 2022) and autocorrelation analysis with the ape R package (Kolowski et al., 2021; Paradis and Schliep, 2019). More details about the camera trap setup and installation are shown in the Supplementary Material (Appendix I).

2.3. Landscape metrics and habitat components

The main habitat components (all tree plantation ages, native forests, and wetlands) were digitalized (1:5000) from satellite Google Earth images from 2020 and afforestation layers of the forestry company. We estimated the percentage of each habitat component at three different buffers centered on the camera trap locations (0.5 km, 1 km, and 2 km radius) to detect possible community and species responses at different scales. Radii were selected to achieve 0.3–0.5 times the maximum known dispersal distances from core areas of the species with the larger and smaller home range, respectively: the Geoffroy's cat *Leopardus geoffroyi* (Castillo et al., 2019; Manfredi et al., 2012) and the white-eared opossum *Didelphis albiventris* (Sanches et al., 2012). Digitalization was performed in QGIS 2.14.15 (QGIS Development Team, 2022).

2.4. Local vegetation survey

In the 26 sampling stations, vegetation structure was measured using a 25-m^2 plot (5x5m plot at 3 m from each camera trap settlement site). The Braun-Blanquet cover-abundance scale (<1, 1–5 %, 6–25 %, 26–50 %, 51–75 %, >75 %) (Braun-Blanquet, 1964, 1932) was used to visually estimate vegetation structure considering the herbaceous, shrub and tree strata. Bare soil cover, leaf litter (composed of *Eucalyptus* leaves within the plantations and by native species leaves in native habitats), and woody debris was also estimated in each plot using the Braun-Blanquet scale. The average tree height (m), trunk height (m), and diameter at breast height -DBH- (m) were measured for all the trees (DAP $\geq$ 2.5 cm) within the plots. The herbaceous height (m) was measured at five random points inside the plot, where herbaceous species were present. A detailed description of vegetation variables is shown in the Supplementary Material (Appendix I, Table S2).

2.5. Data processing

Exifpro image management software (Kowalski, 2013) was used for image processing, tagging species, and extracting picture metadata. The analysis was continued with the camtrapR package (Niedballa et al., 2016) in program R (R Core Team, 2022).

To avoid multiple counting of the same individual at a sampling station, all images of the same species taken over one hour were considered a single independent event. The independence criteria of sampling events over an hour have been considered adequate in similar camera trap studies for medium and large-sized mammals (e.g. Cravino and Brazeiro, 2021; Decarre, 2015; Lantschner, 2012). Livestock records were negligible, so they were not considered for diversity or species composition analyses.

2.5.0.1. Species diversity, capture rate, and composition

Using the complete set of detections -independent photos-, we obtained the number of observed species (species richness) and their respective capture rate in tree plantation and native habitat types, and per each stand age. The species relative abundance or capture rate (CR) was calculated as the number of independent events (records) over the sampling effort (camera-nights) (CR units hereafter: records/camera-nights).

2.6. Vegetation and land cover data analysis

2.6.1. Vegetation structure

To describe the variability of vegetation structure among plantation age classes and native habitat types, we carried out a Principal Component Analysis (PCA) (Legendre and Legendre, 1998; Pearson, 1901), including the nine measured variables described previously (i.e., tree height, diameter at breast height, trunk height, foliage cover, woody debris cover, herbaceous height, herbaceous cover, leaf litter cover, and bare soil cover). The first two PCA dimensions represented vegetation structure and complexity. PCA was performed with the R packages FactoMineR (Le et al., 2008) and factoextra (Kassambara and Mundt, 2020).

2.6.2. Land cover heterogeneity

For the main habitat components among the three different buffered areas centered on the camera-trap stations, landscape heterogeneity was estimated as the Shannon-Wiener diversity index (McGarigal et al., 2012; Shannon and Weaver, 1949), using the percentages of land cover types with the R package vegan (Oksanen et al., 2022).

2.7. Mammal diversity analyses

The relationship between the mammalian assemblage structure and the environmental variation was assessed at three levels: gamma -γ- diversity (i.e., regional), alpha -α- diversity (i.e., local), and beta -β- diversity (i.e., variation in species composition) (Magurran, 2004; Whittaker, 1972, 1960). Firstly, we assessed species diversity at the landscape level (gamma), integrating the study area's data among afforestation age classes and native habitat types. Secondly, we evaluated local (alpha) diversity at the camera traps station level as a function of tree plantation stand ages (Ages 1 to 4) and native habitat types as a function of local vegetation structure and landscape characteristics. Lastly, we assessed the variation in species composition across the landscape (beta) as a function of habitat types and environmental gradients. Details of the analysis performed at each level are shown in the following sections.

2.7.1. Gamma diversity (γ)

Gamma diversity (γ-diversity), as the total species diversity in the landscape, was quantified using the complete set of camera stations at two different levels of aggregation, (i) considering tree plantation stages combined versus native habitats, and (ii) each plantation age class and native habitat separately.

We performed coverage-based rarefaction/extrapolation curves to assess survey effort adequacy and to estimate sampling completeness (Chao and Jost, 2012). From abundance-based diversity accumulation curves, we estimated mammals expected diversity in native habitats and tree plantation altogether, also considering each age stage, forests, and wetlands with Hill numbers (^{q}D) (Hill, 1973), taking into account the effective number of species of order *q*, which tailors diversity to sampled abundances (Chao et al., 2014; Jost, 2007). Diversity of order 0 (^{0}D) represents species richness, considering species based on their incidence only, and therefore sensitive to rare species in the sample (Chao et al., 2014). Diversity of order 1 (^{1}D, exponential of Shannon diversity) weights the species according to their relative abundance (Chao et al., 2014). In turn, the second-order diversity (^{2}D, inverse of the Simpson index or evenness index) overweight the species with high relative abundance, i.e., the dominant species in the sample (Chao et al., 2014). Hill Number estimates of gamma diversity were performed with the R package iNEXT (Chao et al., 2014; Hsieh et al., 2020). More details on sampling completeness and diversity estimations are shown in Appendix II of the Supplementary Material.

We performed rank-abundance curves to visualize how mammal communities differ in number and capture rates of species among native habitats and plantation stages with the R package BiodiversityR (Kindt and Cor, 2005).

2.7.2. Alpha diversity (α)

We model richness response to the plantation and native forests at the station level within a generalized linear mixed modeling framework (GLMM) with a Poisson error distribution and log-link function (Zuur et al., 2009). Wetlands were not considered for α-richness modeling due to the reduced sampling size due to stolen camera traps, and for being structurally very different from tree plantation ages and native forests. We parameterized and fitted a full model with all hypothesized predictors and evaluated their influence by means of effect sizes and 95 % CI. The response variable was the number of species observed per station per month. The "habitat type" (factor variable: Ages 1 to 4 and native forests), the landscape metrics "distance to forest" -Dfor- (continuous variable), the variable "% of afforestation" -%Affo- (continuous variable), and "landscape heterogeneity" -LHet- (continuous variable) were included as fixed effects. %Affo was used as a descriptor of landscape composition for each buffer size; Dfor was measured considering the distance of each station to the nearest forest patch as a proxy for the species main habitat source distance. LHet represented the Shannon diversity of land cover types for each buffer size (see 2.6.2), following the habitat heterogeneity hypothesis effect on biodiversity. All models included two random effects due to sampling design and data grouping containing clusters of non-independent observational units, i.e., the grouping variables "month" and "camera station". All continuous variables were scaled to a mean of 0 and standard deviation of 1.

Among landscape variables, %Affo and LHet, to select the best-fit buffer size (0.5 km, 1 km, 2 km) in the model for land cover and heterogeneity variables, we compared the AIC -Akaike Information Criterion- (Akaike, 1969) values of their univariate models and selected the variant with the lowest value. Models with $\Delta AICc \leq 2$ were considered not significantly different, and ecological coherence was used to choose the best model in such cases. The effects and importance of each included variable were assessed by whether the 95 % confidence interval (CI) of their estimates included zero ($p\text{-value} < 0.05$). We conducted standard diagnostic tests for all the models, including plotting residuals against predicted values and explanatory variables. No overdispersion nor deviations from the expected distribution were detected. The models and further assessments were performed with the R packages glmmTMB (Brooks et al., 2017), DHARMa (Harting, 2022), effects (Fox and Weisberg, 2019, 2018), sjPlot (Lüdecke, 2021), MuMIn (Barton, 2022), and emmeans (Lenth, 2022).

2.7.3. Beta diversity (β) and species-site group associations

Beta diversity refers to the variation in species composition among sites (Legendre and De Cáceres, 2013; Whittaker, 1972). We conducted variance partitioning -VP- analyses and a Redundancy Analysis (RDA) on the Hellinger-transformed data matrix (Legendre and Gallagher, 2001) to disentangle the relative contributions of local and landscape structure on species composition. The local factors included the habitat types considering native forests and all tree plantation age stages, whereas the landscape descriptors included distance to forest (Dfor), the proportion of afforestation cover (%Affo), and heterogeneity (LHet). Wetlands were not considered. The significance of the effects was assessed by permutation test for RDA (999 permutations) overall results and each component's conditional and marginal effect based on the differences in residual deviance in permutations of nested models (Legendre and Legendre, 1998). The goodness of fit for the species was also performed, which gives species contributions to beta-diversity (SCBD) (Legendre and De Cáceres, 2013). We excluded sites with no records (two locations) from these analyses.

Within-habitat type dissimilarity (or betadiversity) was assessed with an analysis of multivariate dispersions accounting for compositional heterogeneity across camera sites on the habitat types. We calculated the average distance of the camera trap station within each habitat to the respective habitat centroid in multivariate space generated by the distance matrix. Significance differences among habitats were tested by first finding the centroids for each habitat and then calculating the squared deviations of each site to that centroid. An ANOVA was performed to test if differences within habitats of beta diversity were significant. Tukey's tests were done to assess which habitats differ. The analysis was performed with the R packages vegan (Oksanen et al., 2022) and asbio (Aho, 2021).

To assess species-habitats relationships, we used the indicator value index (IndVal) (De Cáceres and Legendre, 2009; Dufrêne and Legendre, 1997) for assessing the predictive value of each species as an indicator of a combination of site groups, habitats groups in this case (Ages 1 to 4, native forests, and wetlands). The IndVal index range from 0 (no association) to 1 (strongest association) and is calculated as the product of two factors: specificity and sensitivity or fidelity (De Cáceres et al., 2010; De Cáceres and Legendre, 2009). The specificity (A) is the probability of a site being a member of the site-group combination when the species has been found at that site, and the sensitivity/fidelity (B) is a measurement of how frequently the species is found at sites of the site-group combination under study. For each species, the combination of site groups selected and tested for statistical significance (9,999 Monte Carlo iterations) is the one with the maximum correlation strength, returning the group pattern that better matches the species observed data (De Cáceres et al., 2010; De Cáceres and Legendre, 2009). The strength of association analysis was performed with the package indicspecies (De Cáceres and Legendre, 2009).

3. Results

3.1. Vegetation structure

To describe the changes in the vegetation structure during the afforestation cycle compared with native habitats' vegetation physiognomy (Supplementary Material: Appendix II, Figure S3), we performed the PCA shown in Fig. 2. The first two axes of PCA explained 75 % of the variation in habitat structure (Fig. 2). Stations within each of the four stand age categories, and native habitats had more similar vegetation structures than among categories. Dimension 1 (Dim1) represents a gradient from herbaceous-dominated vegetation (high herbaceous cover and height) towards tree-dominated vegetation of increasing tree cover, trunk height, tree height, and DBH. Dimension 2 (Dim2) describes a gradient from an unvegetated environment with high percentages of bare soil towards a complex vegetation structure with increasing herbaceous cover, tree height, and DBH. Plantation ages were chronologically discriminated along Dim1 from left to right, and Age 1 was also clearly discriminated by low values in Dim2. Age 1 was characterized by higher bare soil cover (Fig. 2, low left panel), Age 2 by higher complexity due to higher herbaceous height and cover (Fig. 2, high left panel), and Ages 3 and 4 by increasing tree height and cover, trunk height, and debris cover (Fig. 2, right panel) (i.e., higher values according to plantation aging). Forests occupied an intermediate position along Dim1, between wetlands and mature plantations of Ages 3 and 4, but closer to plantations of Age 2, that are included in the forest vegetation structure. Wetlands were discriminated, characterized by the higher cover and height of herbaceous vegetation, so thereafter, wetlands were not considered in the performed alpha and beta diversity analyses. Additional information can be found in the Supplementary material (Appendix II, Table S3 and S4, Figure S3 and S4).

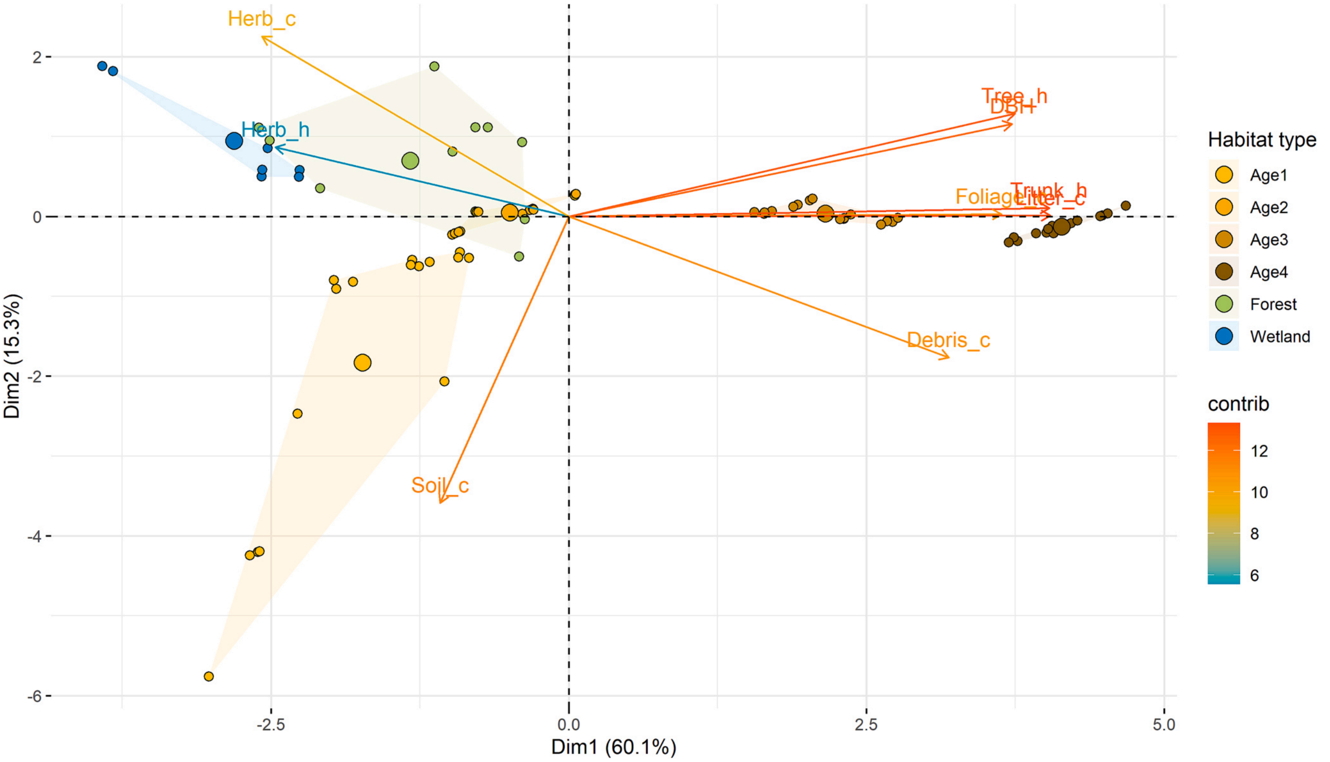

Fig. 2. Biplot from principal component analyses (PCA) of vegetation structure variables along *Eucalyptus* plantation cycle and native habitats. The first two axes explained ∼ 60 % and ∼ 15 % of the variation, respectively. References: DBH = diameter at breast height, Debris_c = woody debris cover, Foliage_c = foliage cover, Herb_c = herbaceous cover, Herb_h = herbaceous height, Litter_c = leaf litter cover, Soil_c = bare soil cover, Tree_h = tree height, Trunk_h = trunk height. The largest dot represents each group centroid. The contributions of variables (contrib) are expressed in percentage and with a color gradient. More information on vegetation variables is shown in Appendices I and II.

3.2. Gamma diversity (γ)

During systematic surveys, we obtained 3,548 independent mammal records for 16 species (Supplementary Material: Appendix III, Figure S5) in 26 camera stations with a total sampling effort of 19,136 camera-nights. From those 3,548 records, 1,788 corresponded to 13 native mammal species and 1,760 to three exotic species (Supplementary Material: Appendix I, Table S1). The registered species corresponded to 80 % of the potential species for the study area and 70 % of the medium to large-sized terrestrial mammals of Uruguay (González and Martínez-Lanfranco, 2010). Two recorded species were reintroduced in the area for the first time in Uruguay: *Nasua nasua* (2003 and 2010) and *Pecari tajacu* (2017). Of the 16 recorded species, 15 (13 natives and two exotics) were detected in native habitats, whereas 11 (eight natives and three exotics) were on plantations (Fig. 4, Supplementary Material: Appendix I, Table S1).

Half of the total records were obtained in stations located in wetlands (49 %, 1,746 independent records), even though these habitat types represent 8 % of the camera stations and the sampling effort (two stations, 1,472 camera-nights); 26 % (906 records) were from native forests representing 31 % of sampling stations and effort (eight stations, 5,888 camera-nights), and 25 % (896 records) to tree plantations representing 62 % of sampling stations and effort (16 stations, 11,776 camera-nights). According to plantation age, higher records were found in Age 2 (456 records, 51 %), followed by Age 3 (267 records, 30 %), Age 4 (162 records, 18 %), and Age 1 (11 records, 1 %); all ages were equally surveyed (four stations and 2,944 camera-nights each).

Sampling completeness was high and comparable for all the

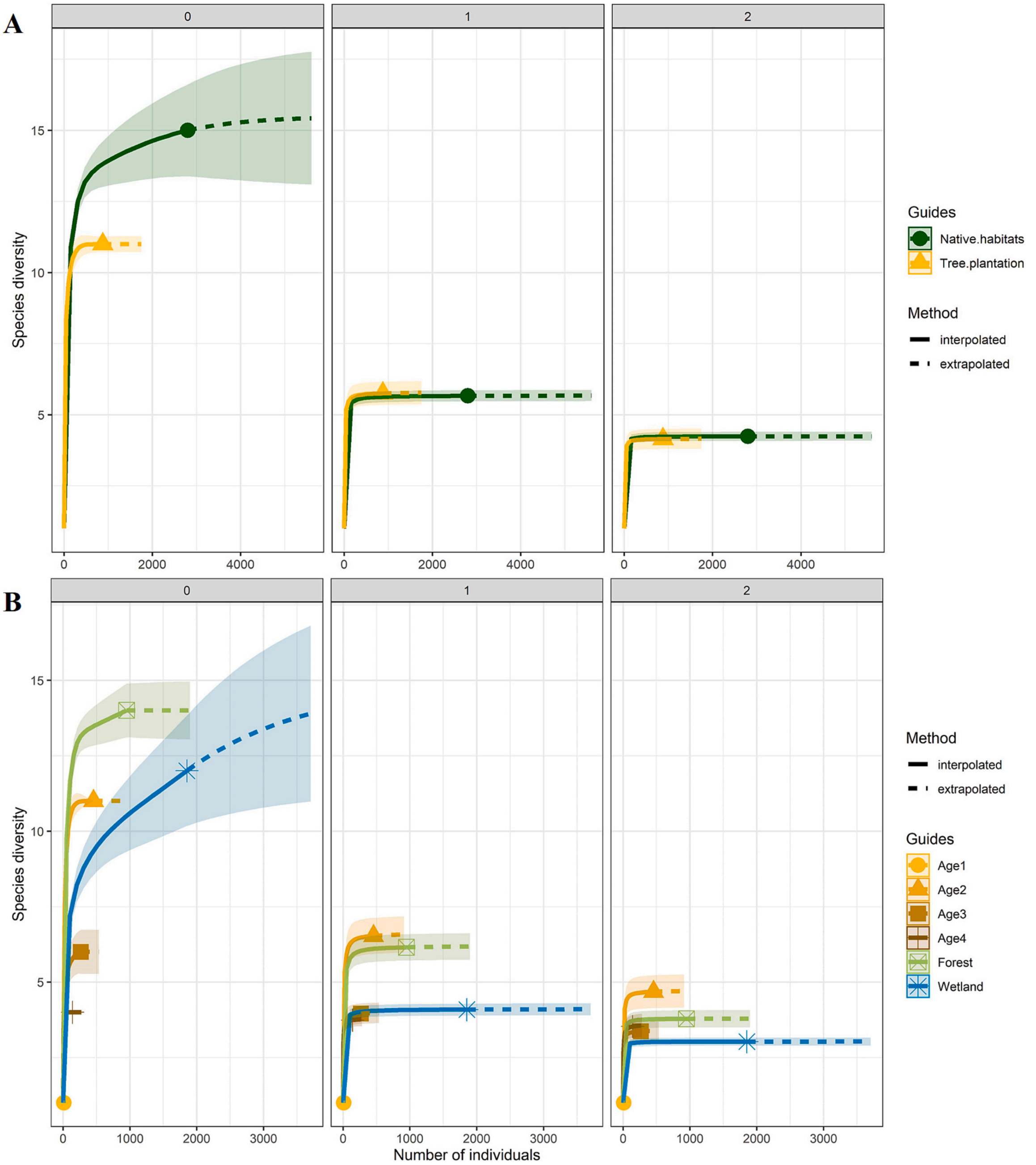

Fig. 3. Individual-based rarefied and extrapolated diversity curves with 95 % confidence intervals (color shade), showing the expected diversity ^{q}D as a function of the number of individuals with q = 0, 1, 2 for A- *Eucalyptus* tree plantations and native habitats collided, and B- tree plantation ages (Age 2, 3 and 4), forests and wetlands separately. Age 1 is represented as a dot since no estimations were performed. Solid icons denote observed diversities in each treatment.

evaluated plantation ages and native habitats (sample coverage > 99 %); more information about sampling completeness is found in the Supplementary Material (Appendix IV, Table S5, Figure S6). No estimations were performed on Age 1 due to the scarce records of a single mammal species.

Hill number results showed that species richness (^{0}D) was significantly different between native habitats (forests and wetlands) and tree plantations, given that the 95 % confidence intervals did not overlap (Fig. 3, left panel); the higher estimated richness value was found in native forests. The curves of Shannon diversity (^{1}D) and dominance (^{2}D) of native habitats and tree plantations were completely overlapped (Fig. 3**A**, middle and right panels).

Considering tree plantations' ages separately, the mammal diversity at Age 2 was significantly different from Age 3 and Age 4 in the three Hill number estimates, given that their 95 % confidence intervals did not overlap with mid to high sampling efforts (Fig. 3**B**). The lowest species richness (^{0}D) was observed at Age 1 (one species), growing rapidly towards the maximum observed richness at Age 2 with 11 species and then decreasing in Ages 3 and 4, with six and four species, respectively. Besides the highest species richness, the mammal assemblage of Age 2 showed the highest Shannon diversity (^{1}D) and dominance (^{2}D) in relation to the other ages, and nearby native forests, especially in ^{1}D. Wetland curves level off beyond the observed diversity, illustrating that higher-order Hill numbers are increasingly dominated by the frequencies of the more common species and are, therefore, less sensitive to sampling effects and with lower evenness.

Species capture rates or relative abundances were significantly higher in native habitats than in tree plantations (Fig. 4). The species capture rate and composition varied during the different stages of the plantations chronosequence, the same as with the main native habitats of the studied landscape (forests and wetlands) (Fig. 4). *Hydrochoerus hydrochaeris* (Hhy) was the most abundant species on wetland stations, and the exotic *Axis axis* (Aax), on tree plantations (all ages) and forest stations (Fig. 4), and the only species recorded in Age 1.

3.3. Alpha diversity (α)

The observed species richness per station ranged from zero to 11 (mean = 5.31 ± 3.60 standard deviation -SD-). Native forest stations had the highest observed mean richness per station (mean = 8.64 ± 3.21 SD), followed by wetland stations (mean = 7.41 ± 4.95 SD). The lowest mean observed richness per station was observed in the tree plantations (mean = 3.94 ± 3.15 SD).

The best model explained 86 % of the variance for both fixed and random effects (Table 1). Species richness was significantly higher in forest stations and stations of Ages 2 to 4, in contrast to Age 1 (Table 1). Among Age 2, Age 3, and native forests, no significant Tukey contrasts were found (Table 1). Landscape variables had no significant effects but

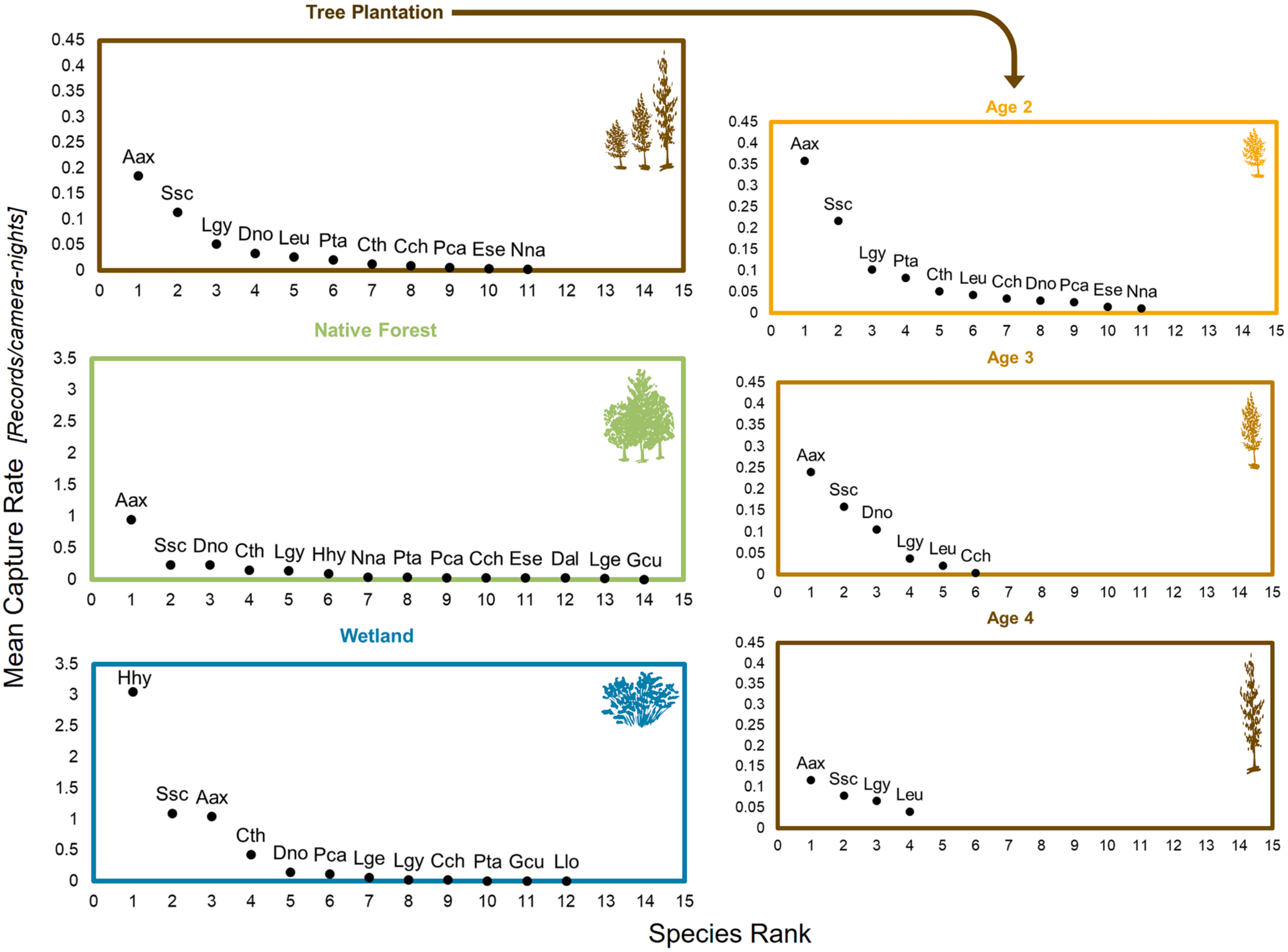

Fig. 4. Rank-abundance plots for mid-large mammals detected in camera traps across native forests, wetlands, and tree plantations -left side-, as well as in Eucalyptus stand ages separately -right side-. Note the different scales in the y-axis between tree plantations and native habitats (forests and wetlands) plots. Age 1 was not considered for plotting due to the lack of records. Species codes are as follow: Aax – *Axis axis*, Cch – *Conepatus chinga*, Cth – *Cerdocyon thous*, Dal – *Didelphis albiventris*, Dno – *Dasypus novemcinctus*, Ese – *Euphractus sexcinctus*, Gcu – *Galictis cuja*, Hhy – *Hydrocherus hydrochaeris*, Lge – *Leopardus geoffroyi*, Leu-*Lepus europaeus*, Llo – *Lontra longicaudis*, Lgy – *Lycalopex gymnocercus*, Nna – *Nasua nasua*, Pca – *Procyon cancrivorus*, Pta – *Pecari tajacu*, Ssc – *Sus scrofa*.

Table 1
Standardized partial regression coefficient and uncertainty estimates from GLMM model of medium-large mammal alpha-level species richness in native forests and tree plantation ages. Model conditional (R^2 cond) -the proportion of the variance explained by both fixed and random effects- and marginal (R^2 marg) -the proportion of the total variance explained by the fixed effects- explained variance, coefficients (Coeff), standard errors (SE) and 95 % lower and upper confidence intervals (LCI, UCI) are shown. Tukey contrast tests were performed for the factor levels of habitat types. Variables and contrasts in bold had a statistically significant effect (p-value < 0.05 and CI not including 0).

Model explained variance			**R^2 cond**	**R^2 marg**
Richness ~ Habitat type + %Aff + LHet + Dfor + (1 | Cam + Month)			0.8591	0.6943
Fixed effects variables	**Coeff**	**SE**	**95 % LCI**	**95 % UCI**
Habitat type: Age 2	**3.3570**	**0.6345**	**2.1134**	**4.6007**
Habitat type: Age 3	**2.8459**	**0.6101**	**1.6501**	**4.0418**
Habitat type: Age 4	**2.1371**	**0.6427**	**0.8775**	**3.3967**
Habitat type: Forest	**2.9622**	**0.6945**	**1.6009**	**4.3234**
% Afforestation (1 km Buffer) -% Aff-	−0.0625	0.2254	−0.3792	0.5042
Landscape heterogeneity (1 km Buffer) -LHet-	0.0935	0.2266	−0.3506	0.5376
Distance to forest (m) -Dfor-	−0.2716	0.1959	−0.6555	0.1123
Factor levels Tukey contrast				
Age 1 - Age 2	**−3.3570**	**0.6345**	**−5.0934**	**−1.6210**
Age 1 - Age 3	**−2.8460**	**0.6101**	**−4.5156**	**−1.1760**
Age 1 - Age 4	**−2.1371**	**0.6427**	**−3.8959**	**−0.3780**
Age 1 - Native Forest	**−2.9622**	**0.6945**	**−4.8628**	**−1.0620**
Age 2 - Age 3	0.5110	0.4470	−0.7111	1.7330
Age 2 - Age 4	**1.2200**	**0.4360**	**0.0279**	**2.4120**
Age 2 - Native Forest	−0.3950	0.3630	−0.5971	1.3870
Age 3 - Age 4	0.7090	0.4420	−0.5019	1.9200
Age 3 - Native Forest	−0.1160	0.5370	−1.5847	1.3520
Age 4 - Native Forest	**−0.8250**	**0.4590**	**−2.0822**	**−0.4320**
Random effects variables	**Variance**	**SE**	**95 % LCI**	**95 % UCI**
Camera station -Cam- (1 to 26)	0.2248	0.4741	0.3154	0.7128
Month (1 to 12)	0.1981	0.4451	0.2779	0.7130

showed either positive (landscape heterogeneity) or negative tendencies (distance to forest, percentage of afforestation) (Supplementary Material: Appendix V, Figure S7).

3.4. *Beta diversity (β) and species-site group associations*

Species composition was significantly different among explanatory variables (R^2 = 0.32; p-value = 2e^{-4}). Species composition was explained by both local and landscape variables (Table 2; Supplementary material: Appendix VI, Figure S7). Habitat type was used as a local factor variable and explained 20 % of species composition (Table 2, Fig. 5). Landscape variables, represented by distance to forest (Dfor), the proportion of afforestation cover within 1 km buffer (%Affo), and landscape heterogeneity (LHet), explained 19 % of species composition (Table 2, Fig. 5). Dfor was significantly associated with species composition (Table 2).

Table 2
Redundancy Analysis (RDA) of variance partitioning for local and landscape variables. Adjusted R^2 and p-values are shown for local and landscape variables aggregated and separately. Significant factors are highlighted in bold (p-value: 0 '***' 0.001 '**' 0.01 '*' 0.05).

Variance partitioning	**Adj. R^2**	**p-value**	
Overall variance	**0.32**	**2e^{-4}**	***
Local Variables	**0.20**	**9e^{-4}**	***
Local Variables | Landscape	**0.08**	**0.014**	*
Habitat type	0.08	0.009	**
Landscape Variables	**0.19**	**3e^{-4}**	***
Landscape Variables | Local	**0.06**	**0.013**	*
% Afforestation (1 km Buffer) -%Aff-	0.02	0.113	
Landscape heterogeneity (1 km Buffer) -LHet-	0.01	0.252	
Distance to forest (m) -Dfor-	**0.03**	**0.049**	*
Shared variance	0.07	Non-testable	

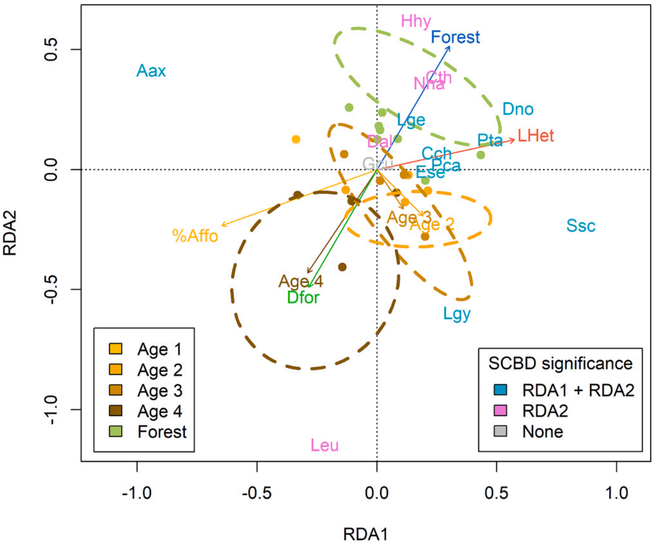

Fig. 5. RDA ordination biplot relating mammal species composition as a function of local (habitat types: Age 1, Age 2, Age 3, Age 4, and Native Forest -Forest-) and landscape-level variables (Dfor, Lhet, %Aff). Points represent camera trap stations per habitat type, delineated by 95 % confidence ellipses. Species contributions to beta-diversity (SCBD) with a goodness of fit ≥ 0.5 are indicated with colors for each species' acronyms. Species codes are shown in Fig. 4.

Within habitat types, species composition showed no significant variation (compositions vary similarly with p-value = 0.2381; Supplementary Material: Appendix VI, Figure S9), while there were significantly different compositions influenced mainly by afforestation cover and distance to forest (Fig. 5; Supplementary Material: Appendix VI, Figures S10 and S11). Distance to forests seems to explain the variation observed within Age 4, represented by the larger hull of the RDA (Fig. 5; Supplementary Material: Appendix VI, Figures S10 and S11).

Except for*Galictis cuja* (Gcu)*,* most species contributed significantly to beta diversity across sites -SCDB- (Fig. 5). Native habitats showed uniqueness in terms of composition along positive scores of both RDA axis (Fig. 5), like *N. nasua* (Nna) and *Cerdocyon thous* (Cth). In turn, some species were primarily associated with plantation stages, scoring high towards negative positions of the second RDA axis (Fig. 5), like *Lepus europaeus* (Leu).

Among the 16 mammal species, 11 (69 %) showed significant indicator values (IndVal: 74–99 %) with different habitat combinations (Fig. 6). Index components for significant associations ranged from 88 to 100 % for specificity -component A- and 57–100 % for sensitivity (naïve occupancy) -component B- (Fig. 6). Age 1 was not considered for habitat correlations due to the lack of records. Age 2 was the plantation stage with a higher correlation to native habitats considering mammal species records.

Native generalist and exotic species are highly associated with larger habitat groups, while the opposite was seen for native specialist species. According to the indicator species analysis results with habitat combinations, *H. hydrochaeris* and *N. nasua* were associated only with wetlands and forests, respectively (Fig. 6). *Leopardus geoffroyi* (Lge) and *C. thous* preferred both native habitats (wetland and forest). All other species had broader habitat preferences, including native habitats and *Eucalyptus* plantations. A. axis was strongly associated with all habitat components, same as *Sus scrofa* (Ssc) excluding Age 4 and *Dasypus novemcinctus* (Dno) with weaker strength. *L. europaeus* was associated with plantations (Ages 2 to 4) while not being recorded in native habitats. *Procyon cancrivorus* (Pca) and *Conepatus chinga* (Cch) were associated with native habitats and Age 2 plantations, and *P. tajacu* (Pta) with that stand age and forests. Additional results are shown in the Supplementary Material (Appendix VII, Table S6).

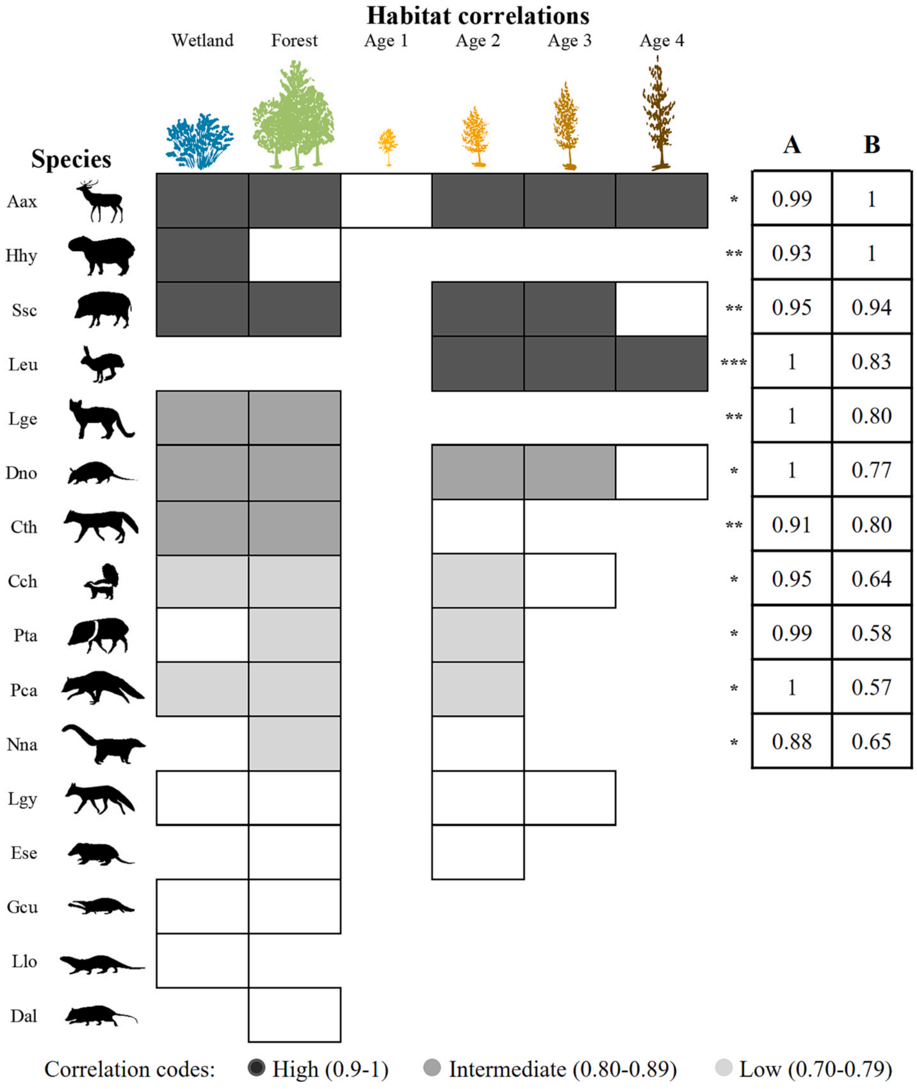

Fig. 6. Strength of species association to afforested and native habitat types from IndVal indicator analysis. Color scale according to IndVal strength between habitats groups and species. White squares represent habitats where the species were found but without species-site correlation. P-value significant code is shown with an asterisk (<0.05 = *, < 0.01 = **, < 0.001 = ***). A and B represent the two IndVal components (specificity and sensitivity, respectively). Species codes are shown in Fig. 4. Silhouettes were vectorized from De Angelo et al. (2017) and the authors' photographs.

4. Discussion

This work found significant differences in mammal diversity and composition within and among the chronosequence of stand age classes and landscape features where plantations were immersed in the region. Consistent with the hypotheses and expectations, local complexity was an important explanatory variable over mammals' richness and composition, but also landscape drivers affected species identities across the afforested study area. Thus, age class stand mosaics, the resulting spatial heterogeneity, and temporal dynamics are essential for local and landscape mammal diversity.

4.1. Vegetation structure

Given the rapid growth rhythm of *Eucalyptus*, especially in plantations for pulp, changes in vegetation structure along the plantation cycle were expected (Tomé et al., 2021; Turnbull, 1999; Wagner et al., 2006). While herbaceous cover declines with age, foliage cover increases, and debris accumulate. This was also seen by Santoandré et al. (2021) in pine plantations ages in a grassland biome from Argentina, where the decline in herbaceous cover was consistent with the increase in canopy cover with increasing age. Considering plant diversity among stands, foliage and litter cover were two of the main factors that led to the decrease of plants in taxonomic and functional diversity through other studied *Eucalyptus* plantation chronosequences (Pairo et al., 2021).

4.2. Mammal species diversity at landscape and local scales

From 16 mammal species detected in our study landscape, 15 were recorded in native habitats (forest and wetland) and 11 in tree plantations. This evidence shows that *Eucalyptus* plantations for pulp production in Uruguay are not "green deserts" (*sensu* Bremer and Farley, 2010) since 69 % of the species were recorded in this new "habitat," indicating that most medium and large-sized mammals make some use of this afforestation. However, we discovered significantly different results when evaluating tree plantations according to their stand age as opposed to when ages were combined.

From the 11 species detected in the *Eucalyptus* plantation, all were recorded in Age 2 stands, but only 55 % were observed in Age 3, 36 % in Age 4, and 9 % in Age 1 (one species). It is noteworthy that the accumulated species richness observed in the young plantations of Age 2 (2 to 4 years) (11 species) was very close to the species number registered in native forests (14 species), which is the highest diversity habitat. About birds in the region, native habitats also exhibited greater diversity and had greater variability in species composition than structurally homogeneous plantations (Martínez-Lanfranco et al., 2022). Andrade-Núñez and Aide (2010) reported a similar pattern of high mammal diversity in *Eucalyptus* plantations in northern Uruguay, resembling a native forest.

Regarding species richness variability at the patch level (alpha diversity), the model fitted showed that local habitat type characteristics and complexity, gathered within the habitat type categories, were the unique factor with significant effects. Species richness was significantly higher in native forest stations and *Eucalyptus* plantations of Ages 2 to 3, in contrast to Ages 1 and 4. The same tendency along ages was found in Brazil (Timo et al., 2015). It is known that alpha diversity tends to decline with land-use intensity (Gibson et al., 2011; Wearn et al., 2019). The influence of the landscape context variables assessed (distance to forest patches, landscape heterogeneity, and percentage of afforestation) over species richness was negligible. Wearn et al. (2019) showed how landscape influence decreases in high-intensity land uses, where local variables gain strength due to fine-scale habitat structure.

However, species richness alone, although being highly used, is not informative about possible changes since it is just a number (Hillebrand et al., 2018), and biodiversity not only consists of richness, it also includes aspects of species identities and dominance. Plantations were dominated by habitat generalists and some forest specialist species, with almost no use by grassland specialists, as in other mammal studies (Cravino and Brazeiro, 2021; Iezzi et al., 2021, 2020; Teixeira et al., 2020; Timo et al., 2015). This was also seen in other animal groups, like butterflies (Casas-Pinilla et al., 2022), reptiles (da Silva Alves Saccol et al., 2017), and birds (Dias et al., 2013; Jacoboski et al., 2016; Jacoboski and Hartz, 2020; Martínez-Lanfranco et al., 2022; Phifer et al., 2017; Vaccaro et al., 2019), but also in plants composition (Pairo et al., 2021).

4.3. Beta diversity (β) and species-site group associations

As for richness, a significant difference in mammal species composition was observed among habitat types. But this variability was partially explained by both local and landscape variables. Once again, the contrasting environmental conditions of patches that emerged from the afforestation cycle are important filters to define species identity at each tree stand age. Among landscape variables, distance to forests in the landscape was influential, especially over Age 4, probably related to this stand age distribution within the landscape. Therefore, besides the local scale, the distances and heterogeneity of the complex mosaic of land cover types, natural and modified, were important since species processes (e.g., foraging, reproduction, movement) occur at different rates within different spatial scales (Addicott et al., 1987; Driscoll et al., 2013; Riva and Nielsen, 2020; Tscharntke et al., 2012). Landscape variables related to geographical distances and their influence on beta diversity could be related to the dispersion ability of the species (Wearn et al., 2019) and were also important in other afforested landscapes (Iezzi et al., 2021). Age 4 stations with shorter distances to forests had a higher number of species, with higher capture rates and different compositions regarding stations with larger distances to forests. When forests were nearby, *S. scrofa* was highly recorded, since forests are the species' preferential habitat (Ruiz, 2017). With fewer forests, *L. europaeus* was found, given that the species prefers less covered areas (Ruiz, 2017).

All species except *G. cuja* (15 from 16) contributed significantly to beta diversity across habitat types, and 11 showed significant indicator values of correlation for a single or a group of habitat types. These emphasized how tightly linked the species are with their habitats. Wetlands and native forests had the highest number of habitat-correlated species (eight-nine species), with only two exotic ones. In *Eucalyptus* plantations, not enough species records were found during the first two years (Age 1), but *L. europaeus* was significantly correlated with the following stages, probably favored by the remaining herbaceous cover (Timo et al., 2015). At Age 2, we found seven indicator species, four native and three exotics. As the plantations grew, the number of indicator species decreased to four and finally to two at Ages 3 and 4, respectively, with an increasing proportion of exotic species. This reinforces the hypothesis that vegetation complexity achieved at Age 2, which resembles the one of native forests, is the key factor explaining the higher biological activity during this stage of the afforestation cycle. Four species had more specialization towards native habitats exclusively: *N. nasua* to forests, *H. hydrochaeris* to wetlands, *L. geoffroyi*, and *C. thous* to both. These four species correspond to habitat specialists (Cravino and Brazeiro, 2021). *C. thous* tend to use forests and forest edges more frequently, but also areas with nearby wetlands (Di Bitetti et al., 2022), and *L. geoffroyi* (Castillo et al., 2019), while *N. nasua* prefers forests with high cover (Desbiez and Borges, 2010). On the opposite, *H. hydrochaeris* presence is highly correlated to wetlands and water sources (Corriale and Herrera, 2014), unlikely to be recorded in tree plantations from other studies (Iezzi et al., 2021, 2020; Timo et al., 2015).

The scarcity of low vegetation at plantations during the earlier and later stages could negatively affect the presence of many mammal species that need understory (Iezzi et al., 2020; Timo et al., 2015), but could not be the only factor since all management activities of the trees occur in those stages (Gabrielle et al., 2013; Montes del Plata, 2019). Many species perceive humans as a predation risk (Gaynor et al., 2021, 2019; Richter et al., 2020). The spatial and temporal risk perception is called the "landscape of fear" and profoundly affects the species ecological interactions along space and time (Gaynor et al., 2019; Laundré et al., 2010, 2001). Species fear perception is based on environmental cues such as human movement, noise, and light intensity, but especially on habitat characteristics: canopy density and understory cover (Verdolin, 2006). Opposite to the mentioned stages, young plantations had significantly more understory vegetation and could offer foraging material and refuge but also a "safety" perception. Last but not least, young plantations also have warmer temperatures due to canopy cover (Santoandré et al., 2021), a condition preferred by mammals (Bennie et al., 2014).

4.4. Concluding remarks and management recommendations

Pulp plantations tend to achieve high canopy cover and low understory as a consequence (Iezzi et al., 2020; Timo et al., 2015; Tomé et al., 2021; Trentini et al., 2017; Turnbull, 1999). This homogeneity within plantation areas could be compensated by maintaining different stand ages, as seen in this work. Tree plantations changed significantly during their cycle. Such variation and its persistence across space and time can help to facilitate the long-term persistence of species by allowing them to move through the shifting landscape. Heterogeneous age plantations would increase landscape mammal diversity and provide more resources for generalist and forest species maintenance. If different ages maintenance is not an option, improving heterogeneity with local management actions, such as promoting native vegetation within and between stands, would be an useful alternative (Athayde et al., 2015; Millan et al., 2015; Prevedello et al., 2018).

Nevertheless, for grassland specialist mammals, management measures considering the maintenance of grassland patches at the landscape level should be emphasized, besides managing the stand-level dynamics. How much remnant grassland area is required to allow specialist mammals persistence in afforested landscapes is still an open question.

CRediT authorship contribution statement

Alexandra Cravino: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration, Funding acquisition. **Juan Andrés Martínez-Lanfranco:** Conceptualization, Software, Formal analysis, Writing – review & editing, Visualization. **Alejandro Brazeiro:** Conceptualization, Formal analysis, Investigation, Resources, Writing – review & editing, Visualization, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120713.

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Supplementary Material for

Community structure of medium-large mammals across a tree plantation cycle in natural grasslands of Uruguay

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This file includes Appendix I-VII, Tables S1-S6, and Figures S1-S11.

Appendix I – Study Area and Methods Details

Study area

In the same study area, native habitats and tree plantations were surveyed. The tree plantation stations were from four different age classes: Age 1 -from 0 up to 2 years-, Age 2 -from 2 up to 4 years-, Age 3 -from 4 up to 7 years- and Age 4 -from 7 to 10 years- (**Figure S1**). Three native forest types (riparian, palm grove, and wooded savanna) and wetlands were the natural habitat components sampled (**Figure S2**).

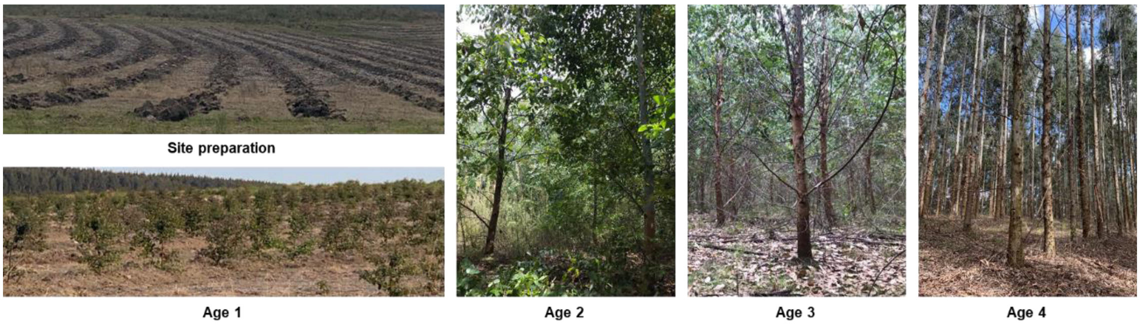
Site preparation
Age 1
Age 2
Age 3
Age 4

Figure S1. Illustrative photographs of the afforestation cycle stages.

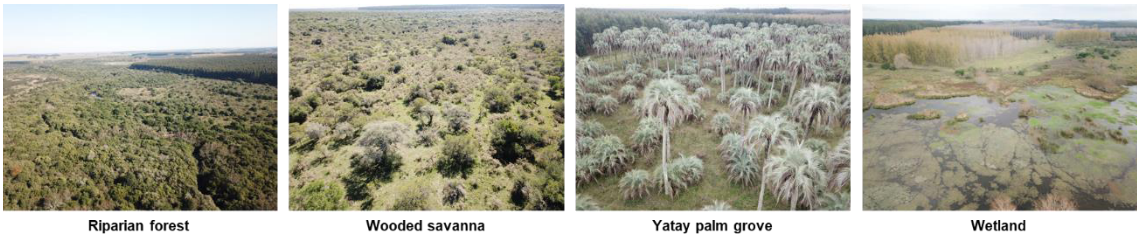
Riparian forest
Wooded savanna
Yatay palm grove
Wetland

Figure S2. Illustrative photographs of the native habitat components.

Mammal species

The regional pool of medium-large mammals in the study areas is restricted to 23 species from 6 Orders and 14 Families. The complete list of potential and observed species is shown in **Table S1**.

Table S1. List of potential and observed mammal species from the study areas. For the species recorded, a reference code (Ref. code) is added.

Order	Family	Scientific name	English common name	Native (N) / Exotic (E)	Recorded	Ref. code
Artiodactyla	Cervidae	*Axis axis*	Axis Deer	E	X	Aax
Artiodactyla	Cervidae	*Mazama gouazoubira*	Gray Brocket	N		
Artiodactyla	Tayassuidae	*Pecari tajacu*	Collared Peccary	N	X	Pta
Artiodactyla	Suidae	*Sus scrofa*	Wild Boar	E	X	Ssc
Carnivora	Canidae	*Cerdocyon thous*	Crab-eating Fox	N	X	Cth
Carnivora	Canidae	*Chrysocyon brachyurus*	Maned Wolf	N		
Carnivora	Canidae	*Lycalopex gymnocercus*	Pampas fox	N	X	Lgy
Carnivora	Felidae	*Leopardus braccatus*	Pampas Cat	N		
Carnivora	Felidae	*Leopardus geoffroyi*	Geoffroy's Cat	N	X	Lge
Carnivora	Felidae	*Leopardus wiedii*	Margay	N		
Carnivora	Felidae	*Puma concolor*	Puma	N		
Carnivora	Mephitidae	*Conepatus chinga*	Molina's Hog-nosed Skunk	N	X	Cch
Carnivora	Mustelidae	*Galictis cuja*	Lesser Grison	N	X	Gcu
Carnivora	Mustelidae	*Lontra longicaudis*	Neotropical Otter	N	X	Llo
Carnivora	Procyonidae	*Procyon cancrivorus*	Crab-eating Raccoon	N	X	Pca
Carnivora	Procyonidae	*Nasua nasua*	South American Coati	N	X	Nna
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded Armadillo	N	X	Dno
Cingulata	Dasypodidae	*Dasypus septemcinctus*	Southern Long-Nosed Armadillo	N		
Cingulata	Euphractidae	*Euphractus sexcinctus*	Yellow Armadillo	N	X	Ese
Didelphiomorphia	Didelphidae	*Didelphis albiventris*	White-eared Opossum	N	X	Dal
Lagomorpha	Leporidae	*Lepus europaeus*	European Hare	E	X	Leu
Rodentia	Caviidae	*Hydrochoerus hydrochaeris*	Capybara	N	X	Hhy
Rodentia	Myocastoridae	*Myocastor coypus*	Coypu	N		

Camera trap set up

The camera traps were active 24 hours a day throughout the sampling period. They were programmed to take three 10-megapixel images upon activation by movement and temperature differences, with a high sensitivity mode and a subsequent 15-second latency. The camera model features a trigger speed of 0.5 seconds. Cameras were installed in trees or poles, facing South or North, to avoid false triggers due to direct sunlight exposure. Baits were not used, and adjacent vegetation that could activate or cover the cameras was removed to optimize detection and facilitate species recognition. The placement height was between 50 and 70cm, according to the average height of potential species, to reduce variations in detectability by body size and/or camera capture angle (Meek et al., 2016). The optimal detection distance was estimated at 3 meters from the placement site.

Vegetation structure variables

Stand-based vegetation measurements of structural components are key to inform on-ground management effects since harvesting, thinning, and weed control are usually implemented at that level (McElhinny et al., 2005). We selected the structure variables shown in **Table S2** to represent the spatial arrangement of different components of the habitat types (stand ages and native habitats) (McElhinny et al., 2005).

Table S2. Vegetation structure variables are considered in selected habitats.

Variable	Reference code	Description
Herbaceous cover	Herb_c	The proportion of area covered by herbaceous – plants without persistent stems or shoots above ground and lacking definite firm structure (Scoggan, 1978) –.
Herbaceous height	Herb_c	Mean height (m) reached by herbaceous species.
Leaf litter cover	Litter_c	The proportion of area covered by leaf litter – small dead plant material that has fallen to the ground –.
Tree height	Tree_h	Mean tree height (m) along the camera trap placing site.
Diameter at breast height	DBH	Mean tree diameter (cm) at breast height – is considered indicative of stand volume and biomass (McElhinny et al., 2005) –.
Tree trunk height	Trunk_h	Mean height (m) reached by the tree trunk – stem and main wooden axis of a tree – until the first branches.
Foliage cover	Foliage_c	The proportion of area covered by tree foliage.
Woody debris cover	Debris_c	The proportion of area covered by woody debris – fallen dead trees and the remains of large branches on the ground/water –.
Bare soil cover	Soil_c	The proportion of area covered by bare soil – an area without vegetation –.

Appendix II – Vegetation structure

Vegetation metrics considering all habitat types (tree stand ages, forests, and wetlands) changed during the surveys. How these metrics changed within and between habitat types can be found in **Figure S3**.

During the first two years (Age 1), the plantation was characterized by small trees (0.3-2.5 m) and high bare soil cover, adopting a grassland-shrubs physiognomy. Between 2 to 4 years (Age 2), herbaceous height and cover increase, as well as the tree height (2-7 m), resembling a native forest with dense understory. At Ages 3 (4-7 years) and 4 (7-10 years), tree height increased fast, from 7 to about 16 m, as well as the trunk height and debris accumulation, but herbaceous vegetation and understory were almost absent.

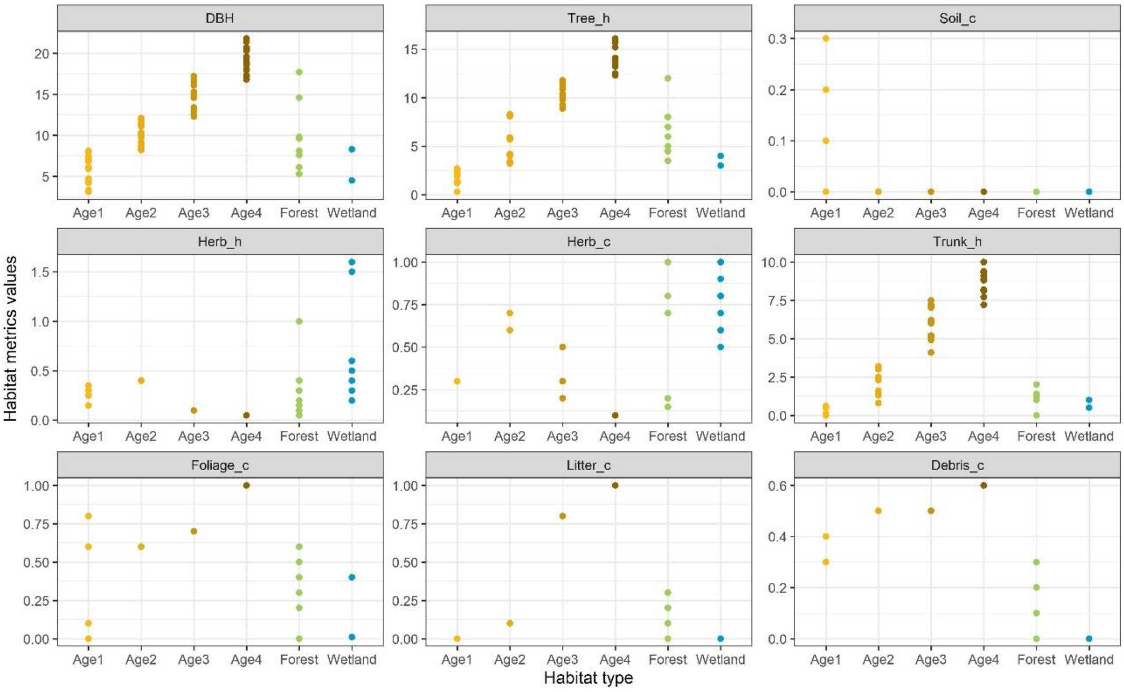

Figure S3. Habitat vegetation metrics values along habitat types: Age 1, Age 2, Age 3, Age 4, Forest, Wetland. DBH is shown in cm, height metrics (_h) in m, and cover metrics (_c) as a proportion. Metrics reference codes are shown in Table S2.

The Principal Component Analysis (PCA) allowed us to summarize and visualize the vegetation information described by multiple inter-correlated quantitative vegetation structure variables from native habitats and plantations. The eigenvalues measure the variation retained by each principal component dimension; when larger than 1, it indicates that the dimension accounts for more variance than one of the single-scaled variables used. This is commonly used as a cutoff point for the dimension's retention, as well as limiting its number to a certain fraction of the cumulative variance explained. Considering that, we selected the first two dimensions (Dim. 1 and Dim. 2) to achieve above 70% of cumulative variance and eigenvalues above one as well (**Table S3**).

Table S3. PCA dimensions eigenvalues and retained variance. Selected dimensions are shown in bold.

PCA Dimensions	Eigenvalue	Variance percent	Cumulative variance percent
Dim. 1	**5.41**	**60.08**	**60.08**
Dim. 2	**1.37**	**15.26**	**75.35**
Dim. 3	0.83	9.17	84.52
Dim. 4	0.55	6.12	90.64
Dim. 5	0.41	4.56	95.20
Dim. 6	0.22	2.45	97.67
Dim. 7	0.14	1.51	99.15
Dim. 8	0.05	0.56	99.73
Dim. 9	0.02	0.27	100.00

Cos2 represents the quality of the representation of the variables. A high cos2 (closer to 1) indicates a good representation of the variable on the principal component dimension. The best representations are found on the first principal component dimension (Dim. 1) (**Figure S4**, **Table S4**).

The variables with higher contribution to Dim. 1 were: leaf litter cover, trunk height, DBH, tree height, and foliage cover (from 16.72 to 13.50%) (**Table S4**). For Dim. 2: bare soil, herbaceous, and woody debris cover (from 51.80 to 12.57%) (**Table S4**).

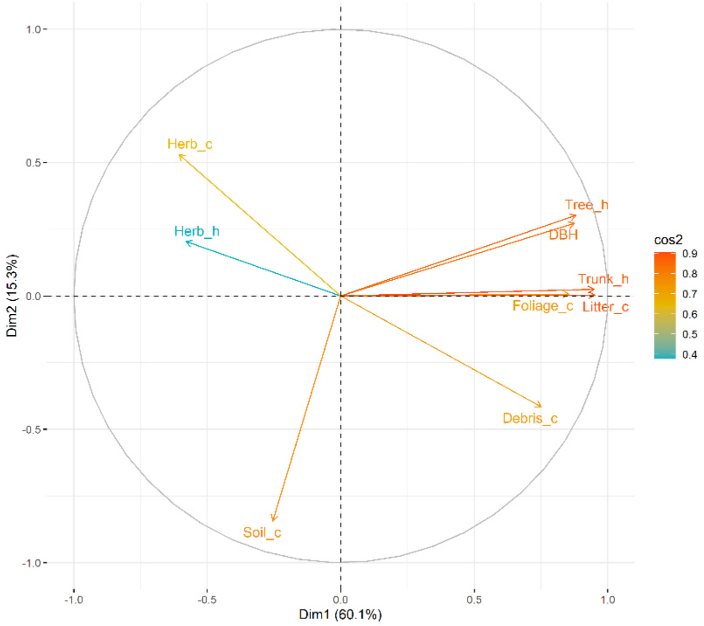

Figure S4. PCA variables correlation plot. The quality of the representation of the variables in the correlation plot (cos2) is shown by the arrow's length (larger indicates best quality of representation) and in colors (orange indicates best quality of representation). Metrics reference codes are shown in Table S2.

Table S4. Quality of representation -cos2- and variables contributions for selected dimensions. Metrics reference codes are shown in Table S2.

Variable	Dim. 1		Dim. 2	
	cos2	Contribution	cos2	Contribution
DBH	0.77	14.16	0.07	5.40
Tree_h	0.78	14.16	0.09	6.66
Soil_c	0.06	1.19	0.71	51.80
Herb_h	0.33	6.20	0.04	3.03
Herb_c	0.36	6.78	0.28	20.5
Trunk_h	0.90	16.65	0.01	0.04
Foliage_c	0.73	13.50	0.01	0.01
Litter_c	0.90	16.72	0.01	0.01
Debris_c	0.56	10.41	0.17	12.57

Appendix III – Mammal assemblage

During surveys, 16 mammal species were recorded with the camera traps. Examples of photographs of different species captured are shown in **Figure S5**.

Figure S5. Example of species recorded on camera traps.

Appendix IV – Sampling completeness and diversity estimations

Sample coverage was even for the stand ages (99.9%) from Age 2 to Age 4 (**Table S5**), implying they are equally complete. For Age 1, no estimations were performed due to the lack of records. All tree plantations -all ages together- and native habitats (forest and wetland) had identical sample coverage values as well (99.9%) (**Table S5**). This is also observed in **Figure S6**.

Table S5. Observed values and diversity estimations for aggregated and separated native habitats (forest and wetland) and aggregated and separated tree plantations (stand ages: Age 2 to Age 4), by Hill numbers of order q (^{q}D): ^{0}D, ^{1}D, and ^{2}D.

	Sample coverage (%)	Diversity	Observed value	Estimated value	Standard error
Native habitats	99.9%	^{0}D	15.00	15.50	1.32
		^{1}D	5.66	5.68	0.10
		^{2}D	4.24	4.25	0.08
Forest	99.9%	^{0}D	14.00	14.00	0.48
		^{1}D	6.15	6.19	0.24
		^{2}D	3.78	3.79	0.20
Wetland	99.9%	^{0}D	12.00	14.09	4.51
		^{1}D	4.09	4.10	0.09
		^{2}D	3.03	3.03	0.08
Tree plantation	99.9%	^{0}D	11.00	11.00	0.09
		^{1}D	5.76	5.79	0.20
		^{2}D	4.15	4.16	0.18
Age 2 -A2-	99.9%	^{0}D	11.00	11.00	0.09
		^{1}D	6.53	6.60	0.30
		^{2}D	4.68	4.72	0.29
Age 3 -A3-	99.9%	^{0}D	6.00	6.00	0.34
		^{1}D	3.95	3.99	0.15
		^{2}D	3.37	3.39	0.18
Age 4 -A4-	99.9%	^{0}D	4.00	4.00	0.00
		^{1}D	3.74	3.78	0.11
		^{2}D	3.53	3.59	0.20

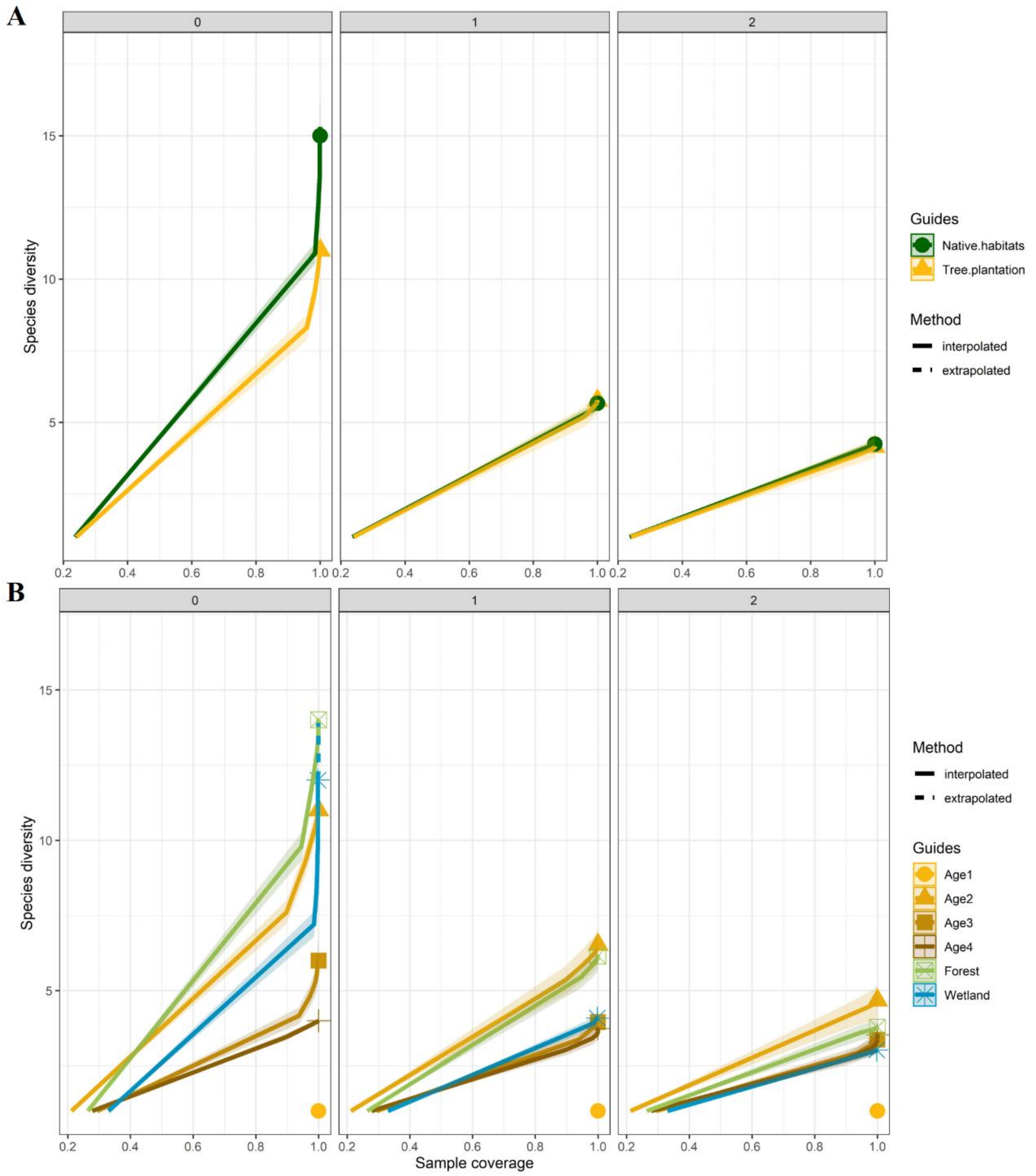

Figure S6. Coverage-based rarefied and extrapolated diversity curves with 95% confidence intervals (color shade), showing the expected diversity ^{q}D as a function of the number of individuals with q = 0, 1, 2 for A- *Eucalyptus* tree plantations and native habitats collied, and B- plantation ages (Age 2, 3 and 4), forests and wetlands separately. Age 1 is represented as a dot since no estimations were performed. Solid icons denote observed diversities in each treatment.

Appendix V – Alpha diversity

Species richness was significantly higher in forest stations and stations of Ages 2 to 4, in contrast to Age 1 (**Figure S7**). Landscape variables had no significant effects but showed positive (landscape heterogeneity) or negative tendencies (distance to forest, percentage of afforestation) (**Figure S7**).

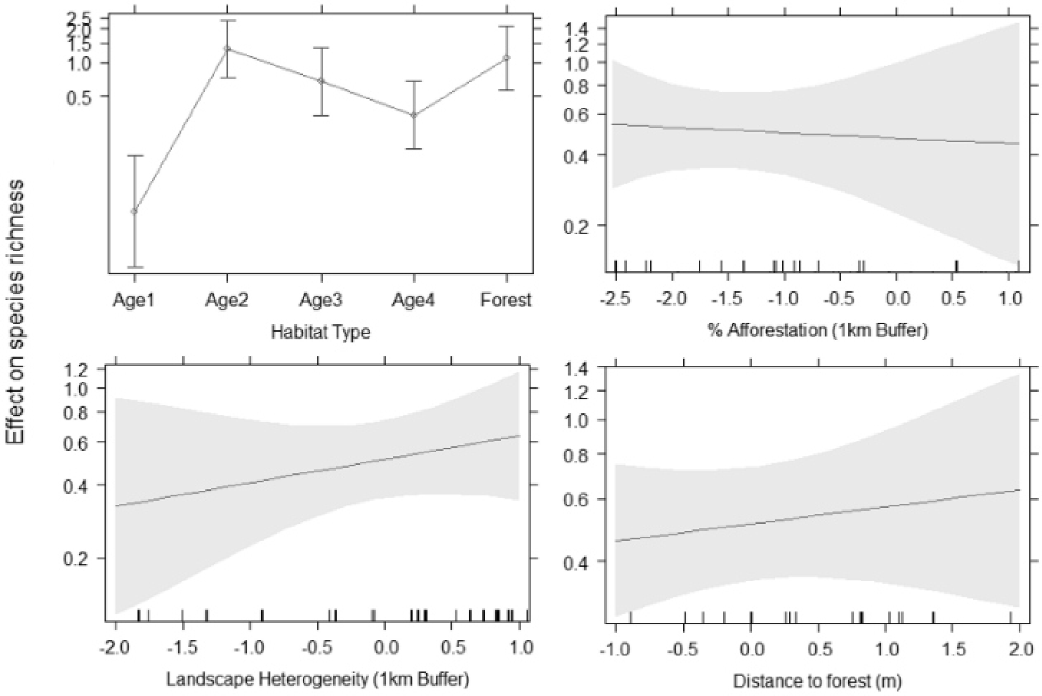

Figure S7. Predicted marginal effects for local and landscape variables on mammal richness per station.

Appendix VI – Beta diversity (β)

Mammal community variation was partitioned using redundancy analyses (RDA) according to local and landscape scale variables, resulting in similar contributions to species composition (**Figure S8**).

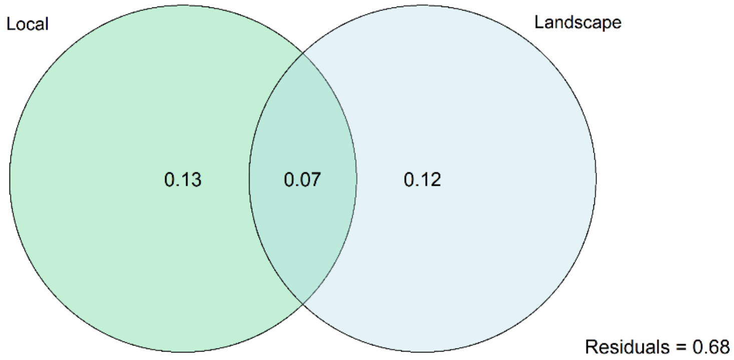

Figure S8. Variation partitioning of the composition of mammal assemblage by local and landscape variables represented with Euler diagrams. Percentage values represent the adjusted coefficient of multiple determination (R^2 adj), and the residual value shown outside the area of the diagram represents the percentage variation left unexplained.

Species composition within habitat types showed no significant variation among group dispersions, as shown in **Figure S9**. But beta diversity from stand ages and forests varied within groups, having significantly different compositions influenced mainly by afforestation cover (**Figure S10**) and distance to forest (**Figure S11**).

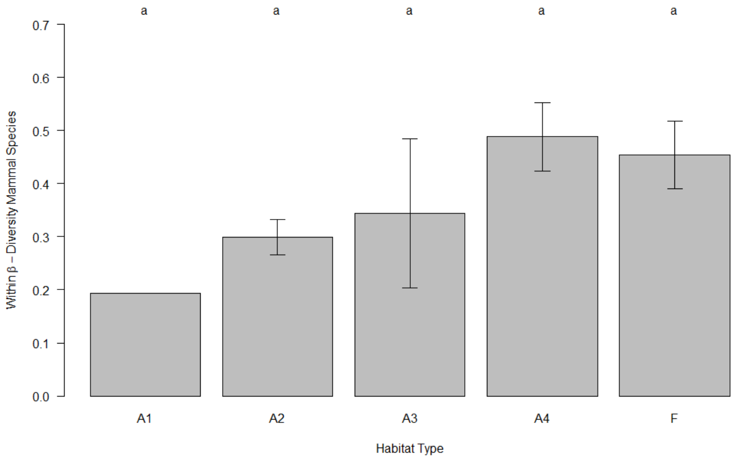

Figure S9. Beta-diversity mammal species. Bars represent mean values with standard errors. The means of habitats with the same letter are not significantly different at alpha = 0.05 using the Tukey HSD method.

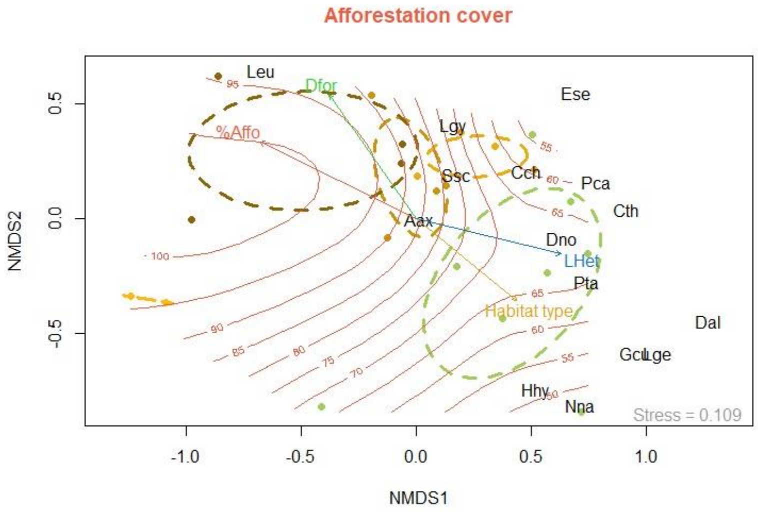

Figure S10. Variations of afforestation cover influence beta-diversity mammal species.

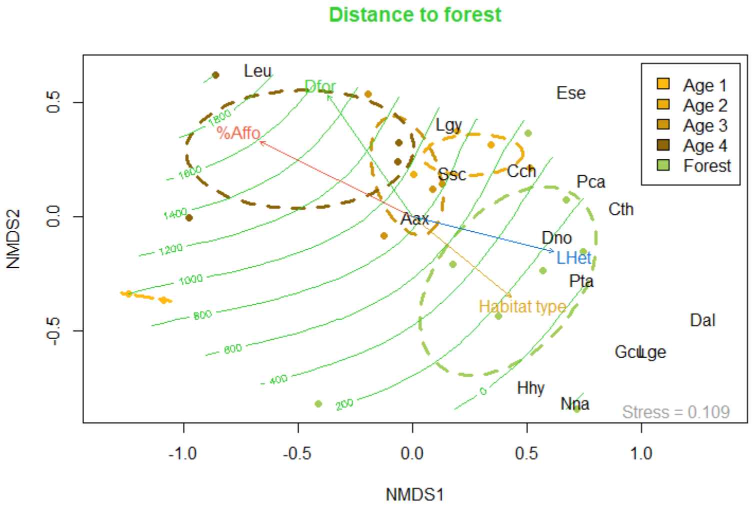

Figure S11. Variations influence beta-diversity mammal species in the distance to forest.

Appendix VII – Species-site group associations

In the Indicator Value Index, component A or specificity is the probability that the surveyed site belongs to the target site group, given that the species has been found (De Cáceres et al., 2010; De Cáceres & Legendre, 2009). Component B, or sensitivity/fidelity, estimates the probability of finding the species in sites belonging to the site group (De Cáceres et al., 2010; De Cáceres & Legendre, 2009). These values give additional information about the species indicator values (Table S6). With B=1, the *Axis axis* and *Hydrochoerus hydrochaeris* can indicate their respective groups because they appeared in all sites belonging to each habitat group (A = 0.99 and 0.93, respectively). In contrast with A = 1, *Lepus europaeus, Leopardus geoffroyi,* and *Dasypus novemcinctus* are good indicators of their habitat groups because they occur in sites belonging to those groups only. However, not all sites within their group include the species (B = 0.83, 0.80, and 0.77, respectively). *Sus scrofa* showed relatively high specificity and fidelity, above 0.9 each. The non-significant correlations, although having high habitat group specificity, showed low sensitivity values (i.e., B=0.50 for *Lontra longicaudis*) being recorded in less than half of the habitat group stations.

Table S6. Species-habitat correlation stats and significance values. A dotted line separates non-significant correlations. Species codes are shown in Table S2.

Species	**Habitat correlations**						**IndVal stat**	**p-value**	**A**	**B**
	Age1	**Age2**	**Age3**	**Age4**	**Forest**	**Wetland**				
Aax	-	1	1	1	1	1	0.996	**0.005**	0.99	1
Hhy	-	0	0	0	0	1	0.964	**0.006**	0.93	1
Ssc	-	1	1	0	1	1	0.946	**0.002**	0.95	0.94
Leu	-	1	1	1	0	0	0.913	**0.001**	1	0.83
Lge	-	0	0	0	1	1	0.894	**0.002**	1	0.80
Dno	-	1	1	0	1	1	0.882	**0.008**	1	0.77
Cth	-	0	0	0	1	1	0.851	**0.004**	0.91	0.80
Cch	-	1	0	0	1	1	0.783	**0.038**	0.95	0.64
Pta	-	1	0	0	1	0	0.758	**0.047**	0.99	0.58
Pca	-	1	0	0	1	1	0.756	**0.045**	1	0.57
Nna	-	0	0	0	1	0	0.743	**0.014**	0.88	0.65
Lgy	-	1	1	1	1	1	0.879	0.069	1	0.51
Llo	-	0	0	0	0	1	0.707	0.093	1	0.50
Ese	-	1	0	0	1	0	0.645	0.165	1	0.41
Dal	-	0	0	0	1	0	0.500	0.586	1	0.25
Gcu	-	0	0	0	1	1	0.447	0.618	1	0.20

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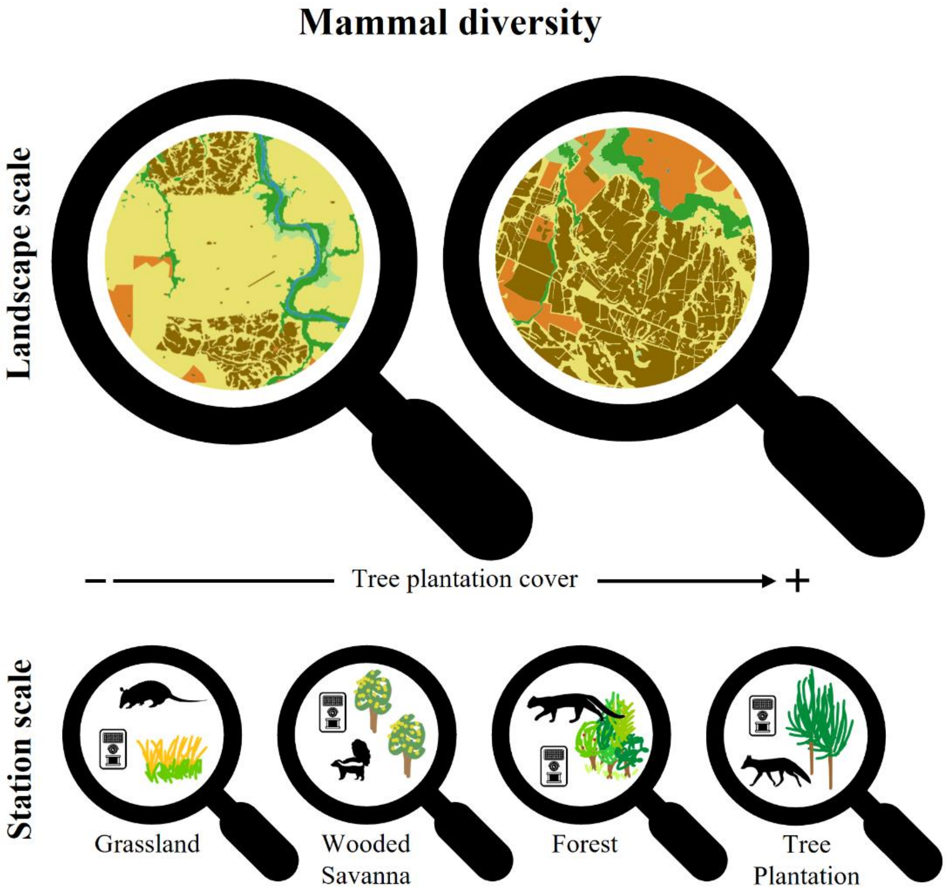
Mamíferos de mediano y gran porte a lo largo de un gradiente de cobertura forestal en los Pastizales del Río de la Plata



Medium-large mammals across a gradient of *Eucalyptus* plantation cover within Río de la Plata Grasslands

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Abstract

Context
Habitat fragmentation is a landscape-scale process involving both habitat loss and habitat partitioning with crucial consequences on biodiversity conservation. The effect of habitat fragmentation on biodiversity is rarely linear and may include tolerance thresholds to species (i.e., transition intervals of fragmentation through which abrupt changes in species viability occur. The Río de la Plata Grasslands region in South America has been experiencing a strong expansion of tree plantations, replacing and fragmenting grasslands.

Objectives
How does the diversity of mammals respond to the afforestation increase in the landscape? Are there species more sensitive to these changes? To address these main questions, we surveyed eight landscapes with different tree plantation cover (6 to 80%) to analyze middle-large-sized mammals' diversity changes in function to land cover and habitat characteristics through several spatial scales.

Methods
Camera traps were deployed within 257 sampling stations among the different habitats (forests, wooded savannas, grasslands, and tree plantations) throughout the eight studied landscapes from 2015 to 2021. Land cover and landscape metrics (edge density and Shannon Diversity Index) were assessed at different radii to analyze the scale of the effects. Species records were used to analyze mammal assemblage's gamma, alpha, and beta diversity changes.

Results
We obtained 5,349 independent mammal species records from 17 species with a total sampling effort of 22,926 camera-nights. Species richness, at local and landscape scales, and local species composition, varied independently from the tree-plantation cover but were positively affected by native forests, grasslands, and landscape heterogeneity. Generalists and some forest species grew in relative abundance as afforestation increased across the landscape, while grassland specialist mammals became less frequent when the grassland cover was reduced to below 40%.

Conclusions
Eucalyptus plantations alter the landscape configuration in Uruguay reducing grasslands cover and increasing edge density. However, medium to large-mammal communities has been slightly affected by afforestation cover. But native habitat patches were key features for species maintenance within the landscapes. Grassland specialists were the most sensitive species, particularly the seven-banded armadillo (*Dasypus septemcinctus*). Thus, this species should be of primary conservation concern for the Uruguayan forestry sector.

Keywords: *Eucalyptus* afforestation, ecological requirements, tolerance threshold, spatial planning

1. Introduction

In recent years, an intense debate about the best strategy to reconcile conservation with production has been unleashed, which demands more and more productive land to supply a growing consumption. This debate has revolved around two alternative strategies: land-sparing versus land-sharing (Green et al. 2005; Phalan et al. 2011; Fischer et al. 2014; von Wehrden et al. 2014; Kremen 2015; Law and Wilson 2015). The first approach consists of separating conservation areas (i.e., national parks) from areas of intensive production of food and goods (Green et al. 2005; Fischer et al. 2014). On the other hand, land-sharing implies producing and conserving biodiversity in the same areas, using wildlife-friendly production methods (Green et al. 2005; Fischer et al. 2014). For many authors, this dichotomous framework does not contribute to the solution of this complex problem since conservation, and sustainable production requires that both strategies work synergistically to balance the management needs for the multifunctionality of landscapes (Perfecto and Vandermeer 2012; Grau et al. 2013; Kremen 2015; Grass et al. 2019). In this context, the configuration of the landscape in terms of composition and integration of natural (conservation-oriented) and productive (production-oriented) patches is key to achieving sharing/sparing connectivity landscapes (Grass et al. 2019).

Human-driven land use and land cover change, which has resulted in habitat loss, fragmentation, and degradation at a very rapid rate, represent a leading driver of biodiversity change (MEA 2005; Newbold et al. 2015, 2016; Graham et al. 2019). Habitat fragmentation is generally defined as a landscape-scale process involving both habitat loss and habitat partitioning leading to landscape configurational changes. Empirical studies suggest that habitat loss has more significant adverse effects on biodiversity (Fahrig 2003; Ewers and Didham 2006). In contrast, habitat partitioning (fragmentation *per se*) seems to have much weaker effects on biodiversity, which are equally likely to be positive or negative depending on the species or group of species considered (Fahrig 2003; Ewers and Didham 2006). Habitat loss and fragmentation usually have non-linear effects on biodiversity, involving critical or tolerance thresholds (Swift and Hannon 2010). Thresholds, defined by turning points, are transition intervals through which small changes in spatial patterns may produce abrupt changes in ecological responses (Turner and Gardner 1991; With and Crist 1995; Fahrig 2003; Ewers and Didham 2006; Swift and Hannon 2010; Thompson 2011). But at what point do habitat modifications disrupt landscape diversity reaching the threshold?

These thresholds are not an inherent property of landscapes but arise from the interaction between species and landscape structures, becoming both species-specific and landscape-specific (With and Crist 1995; Fahrig 2003; Ewers and Didham 2006). Identifying the areal extent (scale) within which landscape variables best explain species' spatial patterns, referred to as the scale of effect (Jackson and Fahrig 2012), is crucial to understand the spatial scale at which wildlife interacts with habitat or landscape traits (Jackson and Fahrig 2012). Likewise, precise scales of effect are essential for implementing management measures over the extent needed for species maintenance.

Particularly, tree plantations with exotic species for wood production or pulp are a productive activity in global expansion, which drives the transformation of natural, semi-natural, or productive land (i.e., under other productive uses) into monospecific tree plantations (FAO 2019). In temperate South America, the conversion of natural grasslands into crops and tree plantations (i.e., afforestation) has reached outstanding levels, especially in the Río de la Plata Grasslands (RPG) (Jobbágy et al. 2006; Baldi and Paruelo 2008; Gautreau 2014; Veldman et al. 2015; Leidinger et al. 2017; Gorosábel et al. 2020). Uruguay, fully immersed within the RPG (Soriano 1991; Paruelo et al. 2007), has experienced a strong expansion of grassland afforestation (*Eucalyptus* and *Pinus*); during the last 30 years, going from less than 2,000 km^2 before the 1990s, to more than 12,000 km^2 in 2019, covering 5.6% of the Uruguayan territory (DIEA-MGAP 2019).

The local effects of grasslands afforestation upon biodiversity have been widely described in the region, with plants (Pairo et al. 2020), insects (Casas-Pinilla et al. 2022), birds (Dias et al. 2013; Dotta et al. 2015; Jacoboski et al. 2016; Phifer et al. 2017; Brazeiro et al. 2018; Vaccaro et al. 2019; Jacoboski and Hartz 2020; Martínez-Lanfranco et al. 2022) and mammals (Dotta and Verdade 2011; Timo et al. 2015; Brazeiro et al. 2018; Iezzi et al. 2020, 2021; Cravino and Brazeiro 2021). These antecedents show that tree planted stands are not "green deserts" (sensu Bremer and Farley 2010) because some species use this new ecosystem, but species richness and frequencies are typically lower than the observed at the original habitats (e.g., Brazeiro et al. 2018; Cravino and Brazeiro 2021; Martínez-Lanfranco et al. 2022). In the case of medium and large-sized mammals in Uruguayan *Eucalyptus* plantations, the richness and relative abundance of species are reduced by 33% and 22% respectively, compared to the replaced native grasslands (Brazeiro et al. 2018; Cravino and Brazeiro 2021). However, little is known about how the effects of tree plantations spread to larger spatial scales (Brazeiro et al. 2018), where other landscape components come into play, such as natural habitats remanent, ecological corridors, or other crops.

How does the diversity of medium-large mammals respond to the afforestation increase in the landscape? Which species are more sensitive to these changes? To address these main questions, we surveyed eight landscapes with different *Eucalyptus* tree plantation cover to analyze mammal diversity changes according to land cover and habitat characteristics through several spatial scales.

2. Methods

2.1. Study area

Uruguay, located in the southeast of South America (30°05′08″-34°58′27″ S, 53°10′58″-58°26′01″ W), has a continental area of 176,215 km². The climate is classified as Humid subtropical -or temperate *sensu* INUMET (INUMET 2020), type "Cfa" *sensu* Köppen-Geiger- (Köppen and Geiger 1926; Beck et al. 2018). According to the official land-cover map of 2015, natural grasslands represent the dominant ecosystem (~60%) in the Uruguayan landscape, with native forests representing 4.8% and other native ecosystems (e.g., wetlands, shrublands) less than 1% (MVOTMA-DINOT 2015). The most widespread productive activity is cattle ranching for meat and dairy, mainly in grasslands (natural and semi-natural) but also in forests, savannas, and some wetlands (DIEA-MGAP 2019). Among anthropic covers, croplands (including artificial grasslands) represent 27.5% of the territory, *Eucalyptus* and *Pinus* afforestation 7.9%, and urban and other artificial areas about 0.8% (MVOTMA 2012).

This study was carried out on one of the main afforested regions of Uruguay, in the Midwest side of the country (**Fig 1**). Within this region, eight landscape samples were studied with camera traps for a year: Bequeló -BE-, Santo Domingo -SD-, El Matorral -EM-, Las Lilas -LL-, Los Arroyos -LA-, Flores -FL-, Rincón del Río -RR-, and Cueva del Tigre -CT-. Within each landscape, four habitat types were surveyed: Tree Plantation -TP-, Forest -FO-, Wooded Savanna -WS-, and Grassland -GS-. Monitored FO were characterized by high values of tree density and canopy cover, while WS had lower values and, therefore more distance between trees. TP were composed of one tree species (i.e., *Eucalyptus dunnii*), from one age class (i.e., mature plantations from 7 to 10 years), and with uniform tree spacing. Afforestation management does not involve thinning (the removal of a proportion of the trees at a certain age to avoid growth competition) or pruning (cutting away dead or overgrown branches or stems from increasing growth). The distance between lines was 3 meters, and the spacing of trees within lines was 3 meters too, with a tree density of 1,111 trees per hectare, with timber regimen (i.e., trees directly planted by seeding or from tree clones planted in each cycle, not by regrowth from the previous plantation cycle). More information on habitat types can be found in the Supplementary Material (Appendix I, Figure S1).

The Uruguayan assemblage of medium-large-sized mammals includes 32 species, 26 natives, and six exotics (González and Martínez-Lanfranco 2010; Grattarola et al. 2016; González et al. 2021). In the studied landscapes, the regional pool of medium-large mammals is restricted to 23 species (20 natives and three exotics), including the Orders Artiodactyla (two natives and two exotics), Carnivora (12 natives), Cingulata (three native species), Didelphiomorphia (one native), Lagomorpha (one exotic) and Rodentia (two natives).

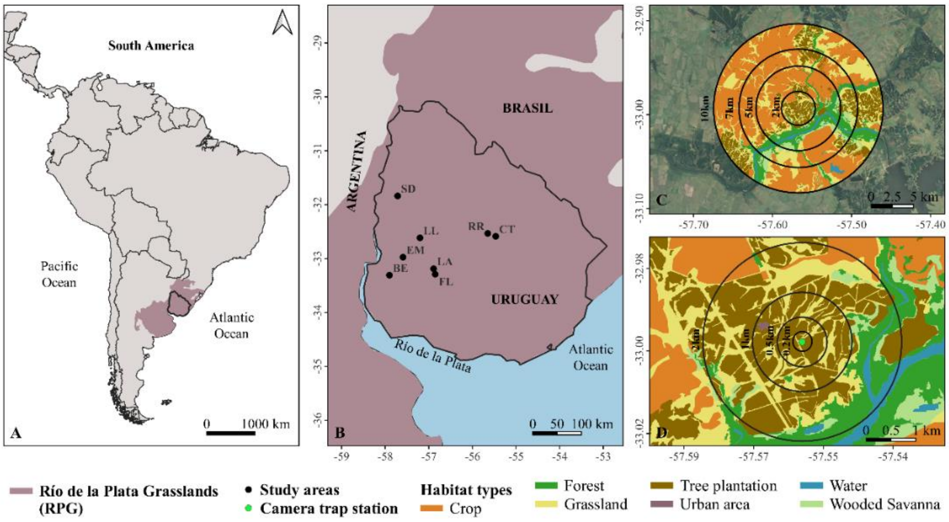

Fig 1 Locations of the eight studied landscapes. (A) The extension of Río de la Plata Grasslands (RPG) in Uruguay and South America is shown in a rosy-brown shade. (B) Location of study areas (BE, SD, EM, LL, LA, FL, RR, CT). (C) Examples of landscape-level buffers (2, 5, 7, and 10km). (D) Examples of camera-level buffers (0.2km, 0.5km, 1km, and 2km). Landcover categories are colored in C and D.

2.2. Sampling design and mammal survey

The sampling design was established to compare the different attributes of the medium and large-sized mammal assemblage between *Eucalyptus* plantations and native habitats among different landscapes. For this purpose, between 2015 and 2021, 257 sampling sites were surveyed continuously for 90 days and then translocated, completing a one-year survey in each landscape, achieving a total effort of 22,926 camera-nights (**Table 1**). In these sites, the surveys were carried out using camera traps (Stealth Cam G42NG) -one per station-which were established following a stratified random sampling design covering *Eucalyptus* mature plantations (TP) and the native habitats (FO, WS, and GR) (**Table 1**).

Camera traps were arranged with a separation of 0.5 km to 1 km (mean distance = 0.71 km, min=0.58 km, max=7.45 km), trying to reduce the probability of detecting the same individuals in different cameras (i.e., independence between stations) and at the same time optimizing the area to be covered. The absence of autocorrelation among stations was additionally confirmed with Moran's Index (p-value>0.05) in the ape R package (Paradis and Schliep 2019; Kolowski et al. 2021). The mapping, selection, and placement of sampling points were performed using QGIS 2.14.15 (QGIS Development Team 2022). More details about the camera trap setup and installation are shown in the Supplementary Material (Appendix I).

Table 1 Sampling effort and camera trap stations among landscapes and habitat types. Sampling effort is expressed as active camera nights. Acronyms of landscapes are shown in **Fig 1**.

Study Sites	Survey Dates	Sampling Effort	Camera Trap Stations per habitat			
			Forest	Wooded Savanna	Grassland	Tree Plantation
FL	2020-2021	2837	8	-	12	-
CT	2016-2017	3348	20	-	7	9
LA	2015-2016	3289	13	2	8	10
RR	2016-2017	3549	28	8	8	10
LL	2015-2016	2503	14	-	11	10
EM	2015-2016	2544	9	10	9	10
SD	2020-2021	2110	8	4	-	8
BE	2020-2021	2746	2	4	5	10

2.3. Landscape metrics and habitat components

The main habitat components (%FO: forest cover; %WS: wooded savanna cover; %GR: grassland cover; %TP: tree plantation cover; %WA: water cover) were digitalized from satellite images (1:5000) from the surveyed years and pre-existing afforestation layers (**Fig 1**). Different buffer radii were selected to compare the effect of landscape structure on the species response at multiple scales to identify the scale of effect. Following Jackson and Fahrig (2012, 2015), as dispersal distance had a strong positive influence on the scale of effect, radii were selected to achieve 0.3-0.5 times the maximum known dispersal distance of the potential species with the larger and smaller home range: the Geoffroy's cat *Leopardus geoffroyi* (Manfredi et al. 2012; Castillo et al. 2019) and the white-eared opossum *Didelphis albiventris* (Sanches et al. 2012). The percentage of each habitat component was measured in four buffers (2, 5, 7, and 10 km) from the centroid of each landscape for further analyses of landscape-level responses. Four other buffers (0.2, 0.5, 1, and 2 km) were centered in every sampling station to detect possible community and species responses at lower scales (station level). Digitalization was performed in QGIS 2.14.15 (QGIS Development Team 2022).

Considering the main habitat components within the four different buffer areas centered on each landscape (2, 5, 7, and 10km), their heterogeneity was estimated with the Shannon Diversity index -SHDI- (Shannon and Weaver 1949), and their tree plantation edge density -ED- (Neel et al. 2004; Martin et al. 2008; Wang et al. 2014) according to the tree stand patches structure with the R package landscapemetrics (Hesselbarth et al. 2019). The SHDI (ranging from 0 -when only one patch is present- and increases as the number of habitats increases while the proportions are equally distributed) at the landscape level is a widely used index for comparing landscapes heterogeneity since its absolute value is not specifically meaningful (McGarigal et al. 2012). Edge density is a function of the amount of border between patches and is one of the most commonly used metrics for quantifying the effects of fragmentation (McGarigal et al. 2012; Wang et al. 2014; Rosa et al. 2017). It is determined by landscape composition and habitat patches and, therefore useful to measure static landscape patterns like afforestation cycles as it standardizes edge to a per unit area basis facilitating comparisons among landscapes of various sizes (Neel et al. 2004; Martin et al. 2008; McGarigal et al. 2012; Wang et al. 2014; Rosa et al. 2017).

Considering the main habitat components among three buffer areas centered on each camera station (0.2, 0.5, 1, 2 km), their heterogeneity (station heterogeneity) was estimated as the SHDI (Shannon and Weaver 1949) according to the percentages of land cover types with the R package landscapemetrics (Hesselbarth et al. 2019).

2.4. Species data processing

Exifpro image management software (Kowalski 2013) was used for image processing, tagging species, and extracting pictures metadata. The analysis was continued with the *camtrapR* package (Niedballa et al. 2016) in program R (R Core Team 2022).

To avoid multiple counting of the same individual at a sampling station, all images of the same species taken over one hour were considered a single independent event. The independence criteria of sampling events over an hour have been considered adequate in similar camera trap studies for mid and large-sized mammals (e.g., Lantschner 2012; Decarre 2015; Iezzi et al. 2020; Cravino et al. 2021). Livestock was not considered within species richness nor subsequent analyses.

Using the complete set of detections -independent photos-we obtained the number of observed species (species richness) and their respective capture rate in tree plantation and natural habitat sites, and per each stand age. The species relative abundance or capture rate (CR) was calculated as the number of independent events (records) over the sampling effort (camera-nights) (CR units hereafter: records/camera-nights).

2.5. Data analysis

2.5.1. Landscape structure

To describe the variability of landcover among the eight surveyed landscapes (landscape level), a Principal Component Analysis (PCA) (Pearson

1901; Legendre and Legendre 1998) was carried out including landcover identified classes, landscape SHDI, and tree plantation ED for the four buffers (2, 5, 7, and 10km) and from average values (see 1.1). This analysis was performed in the R packages FactoMineR (Le et al. 2008) and factoextra (Kassambara and Mundt 2020).

2.5.2. Gamma diversity (γ)

Gamma diversity (γ-diversity) was evaluated at the landscape scale at two levels: multi-habitat gamma diversity (i.e., summing all species in all native habitats and plantations by each studied landscape), and single-habitat gamma diversity (i.e., summing all species by habitat type within each studied landscape). We performed coverage-based rarefaction curves to assess survey effort adequacy to estimate sampling completeness (Chao and Jost 2012; Chao et al. 2020). From abundance-based diversity accumulation curves, we estimated mammal diversity with Hill numbers (${}^{q}D$) (Hill 1973), taking into account the effective number of species of order *q*, which tailors diversity to sampled abundances (Jost 2007; Chao et al. 2014, 2020; Roswell et al. 2021). Diversity of order 0 (${}^{0}D$) represents species richness, considering species based on their incidence only, and therefore sensitive to rare species in the sample (Chao et al. 2014). Diversity of order 1 (${}^{1}D$, exponential of Shannon diversity) weights the species according to their relative abundance (Chao et al. 2014). In turn, the second-order diversity (${}^{2}D$, inverse of the Simpson index or evenness index) overweight the species with high relative abundance, i.e., the dominant species in the sample (Chao et al. 2014). Hill Number estimates of gamma diversity were performed with the R package iNEXT (Chao et al. 2014; Hsieh et al. 2020).

We performed rank-abundance curves to visualize how mammal communities differ in number and capture rates of species among landscapes and their habitat types with the R package BiodiversityR (Kindt and Cor 2005).

2.5.3. Alpha diversity (α)

The response of species diversity (richness) to tree plantation and native covers was modeled separately for each habitat type (FO, GR, WS, TP) at the station level within a generalized linear mixed modeling framework (GLMM) with a Poisson error distribution and log-link function. The response variable was the number of species observed per station. The landscape landcover areas (%FO, %WS, %GR, %TP, %WA) (continuous variables; see 1.1) and the "station SHDI" (continuous variable; see 1.1) of the best-fitted radii size (0.2, 0.5, 1, or 2km) were included as fixed effects. One random effect was included in all models due to sampling design and non-independent observational units, i.e., "landscape". Tree plantation ED was not included for being highly correlated with %TP. Since sampling effort varied among stations, we included the number of nights each camera trap remained active as an offset term in the logarithmic scale in all models. All continuous variables were scaled.

To select the best-fitted buffer sized (0.2, 0.5, 1, and 2km) for landcover and station SHDI variables, we compared the AIC -Akaike Information Criterion- (Akaike 1969) values of their univariate models and selected the variant with the lowest one. For each habitat type, models were then ranked by their AIC, and the model with the lowest value was selected. Models with $\Delta AICc \leq 2$ (Akaike 1969) were considered not significantly different, and ecological coherence was used to choose the best model in such cases. The effects and importance of each variable were assessed by whether the 95% confidence interval (CI) of their estimates included zero ($p\text{-value} < 0.05$). We conducted standard diagnostic tests for all the models, including plotting residuals against predicted values and explanatory variables.

The models and further assessments were performed with the R packages glmmTMB (Brooks et al. 2017), DHARMa (Harting 2022), effects (Fox and Weisberg 2018, 2019), sjPlot (Lüdecke 2021), MuMIn (Barton 2022), and emmeans (Lenth 2022).

2.5.4. Beta diversity (β)

Beta diversity refers to the variation in species composition among sites (Whittaker 1972). We conducted several Redundancy Analysis (RDA) with Hellinger transformation (Legendre and Gallagher 2001) to disentangle the relative contributions of local and landcover structure on species composition for both landscape and station levels. For the landscape level, different RDAs were performed with landcover variables and SHDI from the study area's buffers (2, 5, 7, and 10km; see 1.1). For the sampling stations level, the local factors included were the habitat types from the camera trap locations, whereas the landscape descriptors used were the ones from site buffers and their SHDI (0.2, 0.5, 1, and 2km; see 1.1).

The best landscape and station-level model was selected by forward selection, keeping the statistically but ecologically significant variables and increasing the model's adjusted R^2. The significance of the effects was assessed by permutation test for the different levels RDAs overall results (Legendre and Legendre 2012). The goodness of fit for the species was also performed, which gives species contributions to beta-diversity (SCBD) (Legendre and De Cáceres 2013).

Multiple-site dissimilarity measures accounting for compositional heterogeneity across camera sites on the habitat types were performed to assess spatial patterns of beta diversity within habitat types and landscapes. An ANOVA was performed to test if differences within habitats and landscapes of beta diversity were significant. A Tukey's test was completed to assess if and which habitats and landscapes differ in relation to their variances to evaluate if compositions vary similarly within them. The analysis was performed with the R packages vegan (Oksanen et al. 2022) and asbio (Aho 2021).

3. Results

Eight landscapes with differential land cover areas were surveyed for a year long, achieving high and comparable values of sampling completeness for each of them (sample coverage >99%) according to Hill Numbers estimations (**Table 2**).

3.1. Landscape structure

To describe the changes in landscape structure considering land cover, ED, and landscape SHDI, the PCA with the average variables shown in **Fig 2** was performed. The first two axes of PCA explained 72% of the variation in landscape structure (**Fig 2**). Dimension 1 (Dim1) represents a gradient of tree plantation cover -TP-, from herbaceous-dominated vegetation (grasslands -GR-) towards tree-dominated vegetation of increasing afforestation area and edge density -ED-. Dimension 2 (Dim2) describes a gradient from less native forest cover towards a heterogeneous landscape -SHDI- with increasing cover of forest areas -FO and WS- and water courses -WA- (**Fig 2**). Additional information can be found in the Supplementary material (Appendix II, Table S2 and S3, Figure S3).

Table 2 General species richness along the studied landscapes, their sampling completeness by Hill Numbers estimation (SC), and average landcover percentages (standard deviation is shown in brackets). References: %FO: average rate of forest cover, %WS: average percentage of wooded savanna, %GR: average percentage of grassland, %TP: average percentage of tree plantation, %WA: water, ED: tree plantation edge density vector, SHDI: landscape Shannon heterogeneity vector.

Landscapes	Species richness	SC	Landscape variables						
			%FO	%WS	%GR	%TP	%WA	ED	SHDI
FL	12	1.000	5.7 (3.79)	1.58 (0.41)	73.39 (11.49)	6.35 (3.78)	1.16 (0.19)	19.28 (8.95)	0.9 (0.04)
CT	13	0.998	2.9 (1.18)	0.12 (0.22)	55.07 (3.88)	10.72 (9.88)	0.07 (0.09)	19.95 (11.98)	0.98 (0.07)
LA	14	0.998	7.64 (1.84)	1.97 (0.35)	63.37 (12.51)	16.13 (8.61)	2.18 (0.39)	33.65 (16.04)	1.06 (0.11)
RR	13	0.998	4.36 (0.25)	0.88 (0.66)	41.06 (7.51)	21.77 (8.38)	11.35 (3.08)	36.8 (17.24)	1.4 (0.04)
LL	13	0.990	5.6 (2.68)	0.9 (0.64)	40.78 (7.19)	34.74 (7.43)	0.07 (0.05)	110.78 (26.74)	1.03 (0.21)
EM	11	1.000	10.37 (5.57)	4.74 (1.32)	22.12 (5.84)	39.21 (6.32)	1.9 (1.36)	45.95 (12.2)	1.41 (0.07)
SD	11	1.000	3.99 (0.97)	0.9 (0.47)	25.5 (2.53)	56.81 (5.91)	0.1 (0.09)	63.2 (11.39)	1.25 (0.03)
BE	12	0.996	4.25 (2.84)	1.61 (1.11)	22.5 (2.18)	77.72 (8.8)	0.04 (0.03)	72.2 (13.57)	1.15 (0.28)

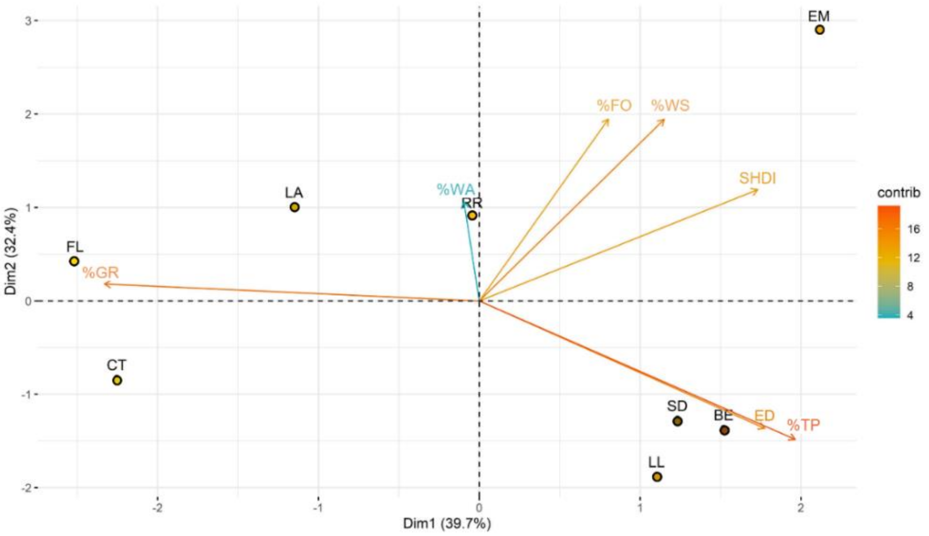

Fig 2 Biplot from principal component analyses (PCA) of landcover, heterogeneity, and tree plantation edge density at the landscape scale. References: %FO- average percentage of forest, %WS- average percentage of wooded savanna, %GR- average percentage of grassland, %TP- average percentage of tree plantation, %WA- water, ED- tree plantation edge density vector, SHDI- landscape Shannon heterogeneity vector. The contributions of variables (contrib) are expressed in percentage and with a color gradient.

3.2. Gamma Diversity (γ)

During systematic surveys, we obtained 5,349 independent mammal species records for 17 species (Supplementary Material: Appendix II, Table S1) in 257 camera stations with a total sampling effort of 22,926 camera-nights. From the total records, 4,080 independent records corresponded to 13 native mammal species and 1,269 to three exotic species (Supplementary Material: Appendix II, Table S1). Of the 17 recorded species, all (14 natives and three exotics) were detected in native habitats, whereas 11 (8 natives and three exotics) were on plantations (**Fig 5**, Supplementary Material: Appendix II, Table S1). Half of the total records were obtained in stations located in FO (49%, 2,617 independent records), 29% (1,533 records) were from GR, 11% (698 records) from WS, and 9% (501 records) from TP.

3.2.1. Mammal diversity estimations

Hill numbers' results considering landscapes showed that species richness (^{0}D) was not significantly different between the eight study areas (i.e., multi-habitat gamma diversity), given that the 95% confidence intervals overlapped (**Fig 3**), although the higher observed and estimated richness value was found in intermediate plantation cover (CT, LA, RR, LL). The curves of Shannon diversity (^{1}D) and dominance (^{2}D) overlapped entirely, except for the grassland-dominated area (FL) and from the one higher TP cover (BE), being significantly different (**Fig 3**). The grassland-dominated landscapes showed the highest diversity for ^{1}D (common species) and ^{2}D (dominant species), while the most afforested landscapes had the lowest values. More information on estimations and sampling completeness can be found in the Supplementary Material (Appendix IV, Table S4, Figures S4).

With respect to single-habitat gamma diversity (FO, WS, GR, and TP), the mammal diversity estimators ^{0}D in FO were higher than in the other habitat types. The highest values from FO were in the intermediate afforested landscapes (**Fig 4**). GR was the second most diverse habitat type, especially in grassland-dominated landscapes (**Fig 4**). The third diversity position was for WS (**Fig 4**), with no significant differences among landscapes with completely overlapped confidence intervals, followed by TP. Among landscapes, TP in the highest afforested area (BE) had significantly higher diversity (**Fig 4**). More information on ^{1}D and ^{2}D is shown in the Supplementary Material (Appendix IV, Figures S5-S8).

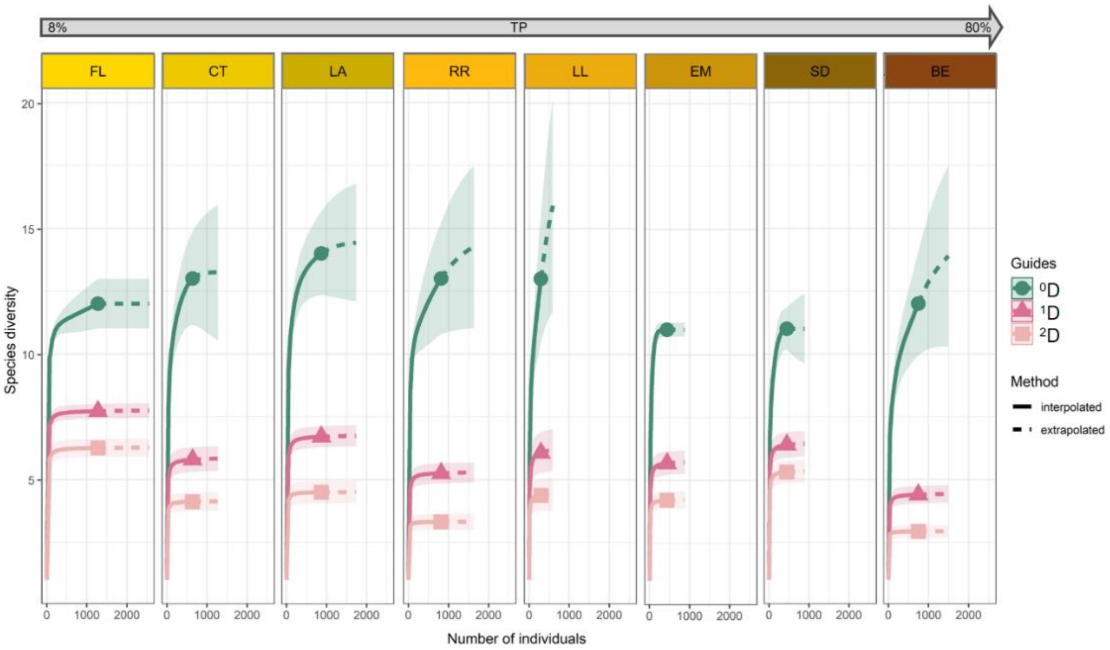

Fig 3 Multi-habitat gamma diversity. Sample-based diversity rarefaction and extrapolated curves with 95% confidence intervals (color shade), showing the expected diversity ^qD as a function of the number of individuals with q = 0, 1, 2 for eight studied landscapes with different tree plantation cover (ranging from lowest to highest: FL, CT, LA, RR, LL, EM, SD, BE). Solid icons denote observed diversities in each treatment.

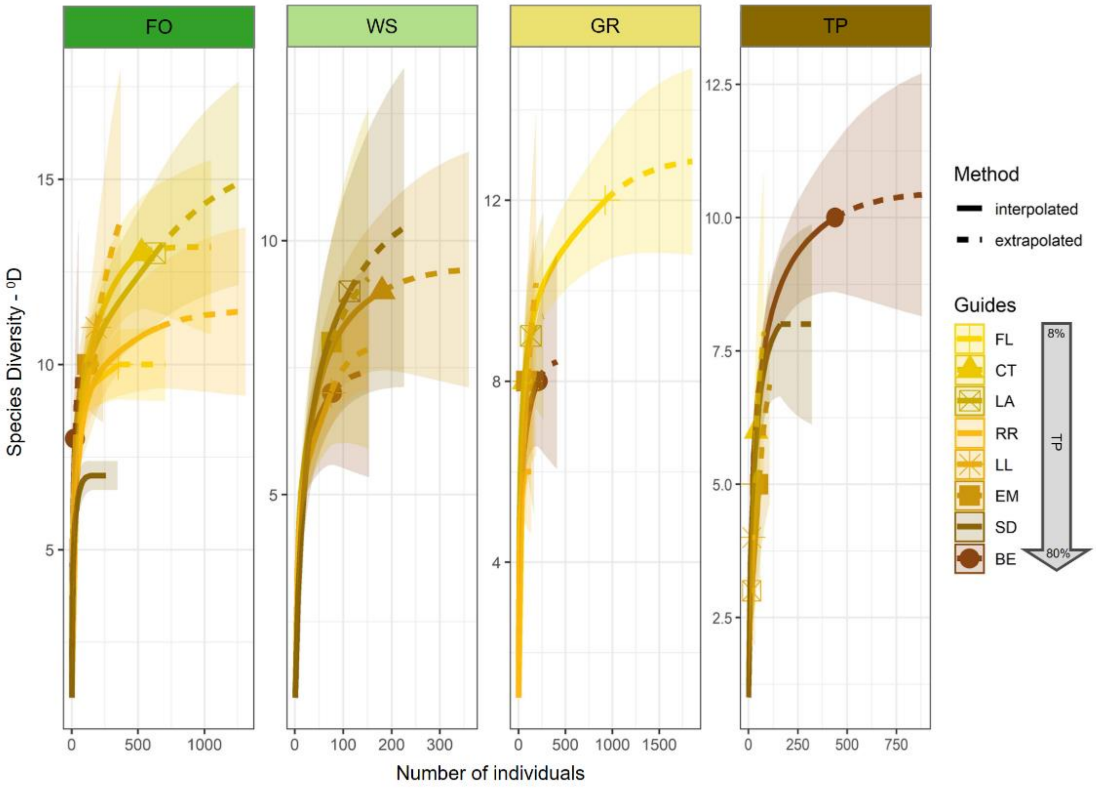

Fig 4 Single-habitat gamma diversity. Sample-based diversity rarefaction and extrapolated curves with 95% confidence intervals (color shade), showing the expected diversity ^qD as a function of the number of individuals with q = 0 for habitat types (FO, WS, GR, and TP) within afforested landscapes (ranging from lowest to highest: FL, CT, LA, RR, LL, EM, SD, BE). Solid icons denote observed richness in each treatment. Note the different scales in the y-axis plots. References: FO- Forest, WS- Wooded savanna, GR- Grassland, TP- Tree plantation.

3.2.2. Rank-abundance curves

The species capture rate and composition varied across the different landscapes (**Fig 5**, **Fig 6**), the same as with the main native habitats within them (Supplementary Material: Appendix IV, Figure S9). Higher capture rates from all species, were recorded in the grassland-dominated landscape (FL), where the exotic European hare *Lepus europaeus* and the pampas fox *Lycalopex gymnocercus* were the dominant species (**Fig 5**, **Fig 6**). The seven-banded armadillo *Dasypus septemcinctus* was almost exclusive of this landscape with 119 records since only seven were found in the afforested ones, up to 40% of remanent GR (**Fig 5**, **Fig 6**). The exotic Axis Deer, *Axis axis*, was the most frequent species on landscapes with high plantation cover (SD and BE) (**Fig 5**, **Fig 6**). In landscapes from 10 to 40% (CT, LA, RR, LL, EM) TP cover, the most frequent species were *L. gymnocercus* or the nine-banded armadillo *Dasypus novemcinctus* (**Fig 5**, **Fig 6**). Some forest specialists remained constant across the landscapes, such as *L. geoffroyi*, while others increased the records, such as the crab-eating fox *Cerdocyon thous* (**Fig 5**, **Fig 6**).

3.3. Alpha diversity (α)

The observed richness per landscape ranged from 11 to 14 species (**Table 3**). As shown for gamma diversity, no significant differences in general richness patterns were found between the eight study areas considering the landscape level (p-value = 0.4289). At the sampling station level, the results were different. The observed species richness per station ranged from 0 to 10 (mean = 4.86 ± 2.12 SD). FO stations had the highest observed mean richness per station (mean= 5.54 ± 2.01 SD), followed by WS stations (mean= 4.04 ± 1.94 SD) and GR stations (mean= 4.49 ± 2.19 SD). The lowest mean observed richness per station was observed in TP (mean= 2.73 ± 1.83 SD).

For FO stations, the best model explained 68% of the variance for fixed and random effects (**Table 3**). Only one landscape variable was kept in the best-adjusted model: the forest cover within a 500m buffer (FO500m), with a significantly positive effect on species richness (**Table 3**, **Fig 7**). For WS stations, the best model explained 71% of the variance for both fixed and random effects (**Table 3**). Two landscape variables were kept in the best-adjusted model: the forest cover and the local heterogeneity within a 500m buffer (FO500m and SHDI500m, respectively), both with a significantly positive effect on species richness (**Table 3**, **Fig 7**). For GR stations, the best model explained 73% of the variance for both fixed and random effects (**Table 3**). Two landscape variables were kept in the best-adjusted model: the forest cover within a 500m buffer (FO500m) and the grassland cover within a 1km buffer (GR1km), both with a significantly positive effect on species richness (**Table 3**, **Fig 7**). For TP stations, the best model explained 79% of the variance for both fixed and random effects (**Table 3**). Only one landscape variable was kept in the best-adjusted model: the tree plantation cover within a 500m buffer (FO500m), with a significantly negative effect on species richness (**Table 3**, **Fig 7**).

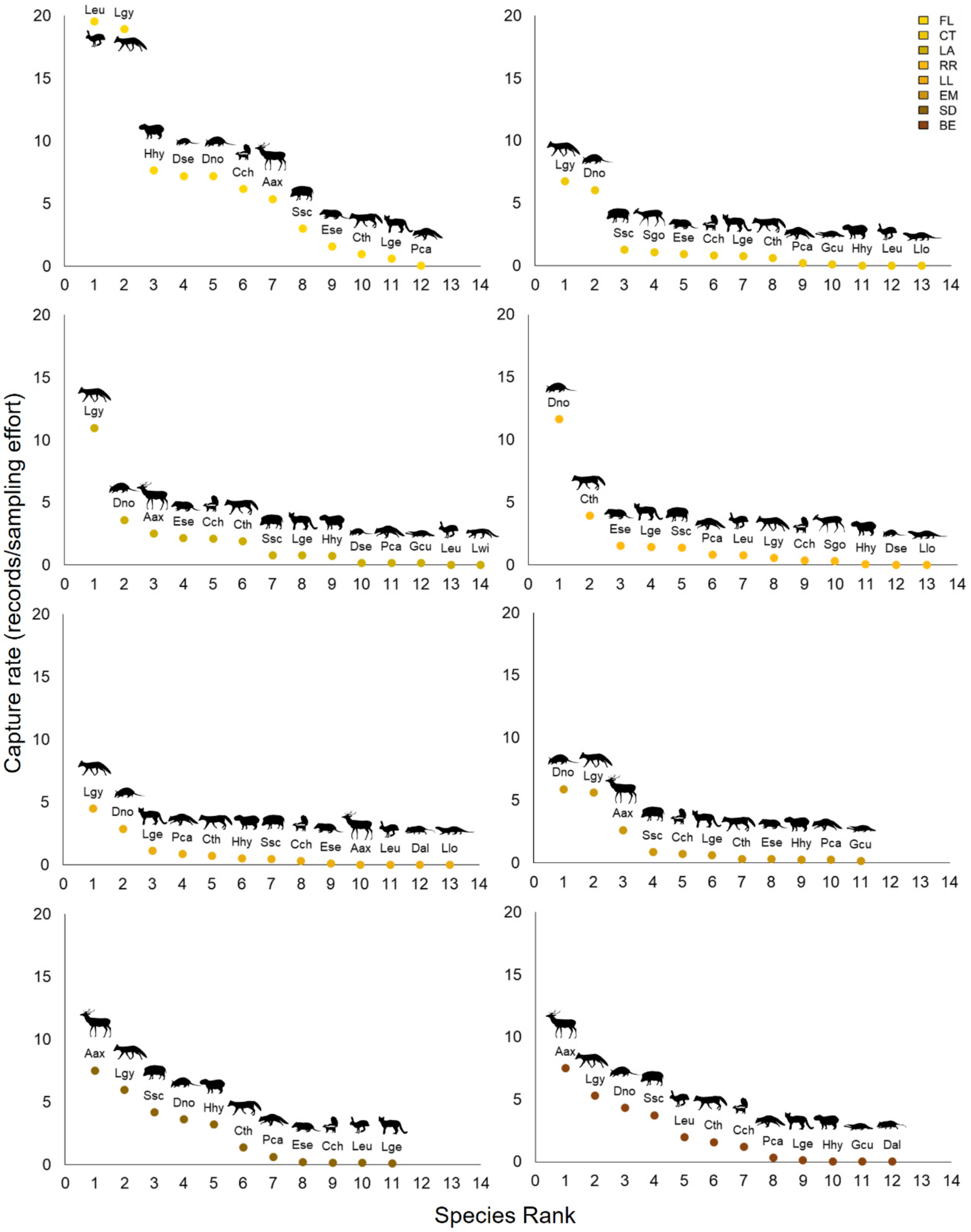

Fig 5 Rank-abundance plots for mid-large mammals detected in camera traps across landscapes with differential plantation cover (ranging from lowest to highest: FL, CT, LA, RR, LL, EM, SD, BE). Species codes are as follow: Aax- *Axis axis*, Cch- *Conepatus chinga*, Cth- *Cerdocyon thous*, Dal- *Didelphis albiventris*, Dno- *Dasypus novemcinctus*, Dse- *Dasypus septemcinctus*, Ese- *Euphractus sexcinctus*, Gcu- *Galictis cuja*, Hhy- *Hydrocherus hydrochaeris*, Lge- *Leopardus geoffroyi*, Leu- *Lepus europaeus*, Llo- *Lontra longicaudis*, Lgy- *Lycalopex gymnocercus*, Lwi- *Leopardus wiedii*, Pca- *Procyon cancrivorus*, Ssc- *Sus scrofa*, Sgo- *Subulo gouazoubira*.

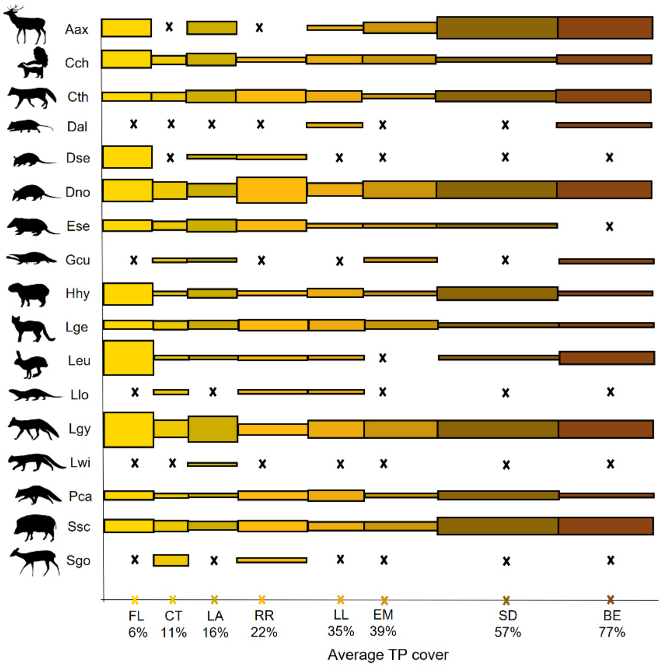

Fig 6 Gradient of species frequencies detected in camera traps across landscapes with differential TP cover (ranging from lowest to highest: FL, CT, LA, RR, LL, EM, SD, BE). Species codes are shown in **Fig 5**.

Table 3 Standardized partial regression coefficient and uncertainty estimates from GLMM model of mammal alpha-level species richness at station level considering different afforested landscapes (Land; FL, CT, LA, RR, LL, EM, SD, BE). Model conditional (R^2 cond) -the proportion of the variance explained by both fixed and random effects- and marginal (R^2 marg) -the proportion of the total variance explained by the fixed effects- variance, coefficients (Coeff), standard errors (SE) and 95% lower and upper confidence intervals (LCI, UCI) are shown. Tukey contrast tests were performed for the factor levels of habitat types. Variables and contrasts in bold had a statistically significant effect (p-value<0.05 and CI not including 0). References: FO500m- forest within 500m buffer, SHDI500m- Shannon Diversity local heterogeneity cover within 500m buffer, TP500m- tree plantation within 500m buffer, GR1km- grassland within 1km buffer.

Forest stations (FO)				
Model explained variance			**R^2 cond**	**R^2 marg**
Richness ~ FO500m + (1 | Land)			0.68	0.59
Fixed effects variables	**Coeff**	**SE**	**95% LCI**	**95% UCI**
FO500m	**0.14**	**0.05**	**0.05**	**0.25**
Random effects variables	**Variance**	**SE**	**95% LCI**	**95% UCI**
Land	0.11	0.05	0.01	0.38
Wooded Savanna stations (WS)				
Model explained variance			**R^2 cond**	**R^2 marg**
Richness ~ FO500m + SHDI500m + (1 | Land)			0.71	0.61
Fixed effects variables	**Coeff**	**SE**	**95% LCI**	**95% UCI**
FO500m	**0.20**	**0.08**	**0.03**	**0.43**
SHDI500m	**0.37**	**0.08**	**0.07**	**0.41**
Random effects variables	**Variance**	**SE**	**95% LCI**	**95% UCI**
Land	0.11	0.07	0.10	0.43
Grassland stations (GR)				
Model explained variance			**R^2 cond**	**R^2 marg**
Richness ~ FO500m + GR1km + (1 | Land)			0.73	0.67
Fixed effects variables	**Coeff**	**SE**	**95% LCI**	**95% UCI**
FO500m	**0.10**	**0.09**	**0.02**	**0.26**
GR1km	**0.22**	**0.09**	**0.03**	**0.41**
Random effects variables	**Variance**	**SE**	**95% LCI**	**95% UCI**
Land	0.07	0.04	0.05	0.49
Tree Plantation stations (TP)				
Model explained variance			**R^2 cond**	**R^2 marg**
Richness ~ TP500m + (1 | Land)			0.79	0.71
Fixed effects variables	**Coeff**	**SE**	**95% LCI**	**95% UCI**
TP500m	**-0.28**	**0.11**	**-0.51**	**-0.05**
Random effects variables	**Variance**	**SE**	**95% LCI**	**95% UCI**
Land	0.09	0.03	0.02	0.79

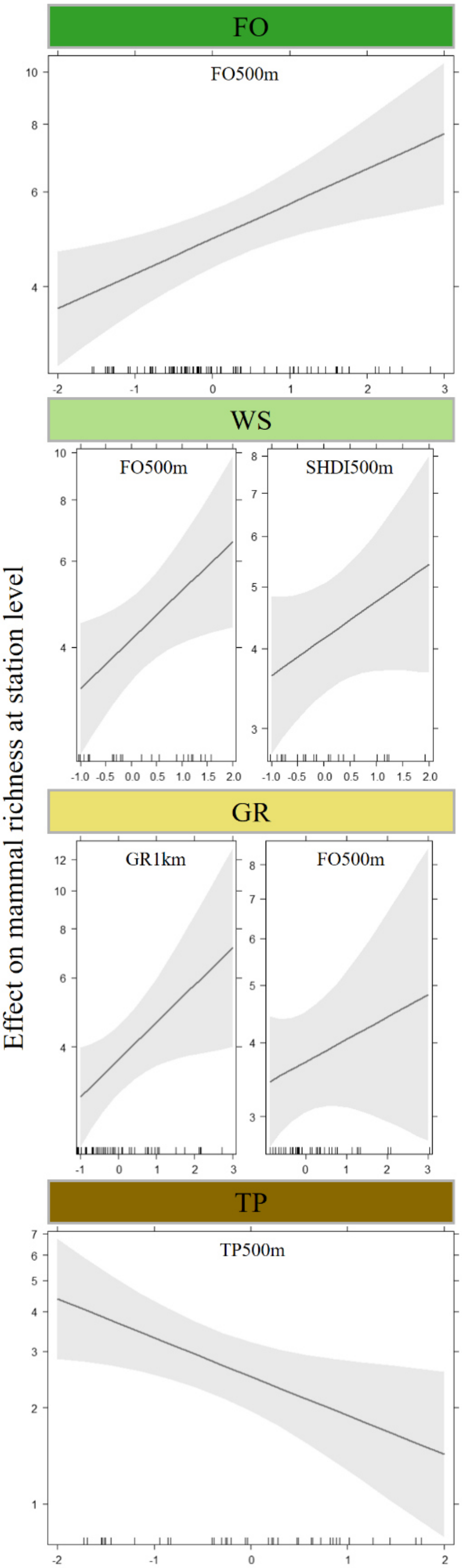

Fig 7 Predicted marginal effects of habitat types and landscape variables at station-level on mammal richness for the different habitat types (FO, GR, WS, TP).

3.4. Beta diversity (β)

Species composition differed significantly at the landscape (R^2=0.45, p-value=0.038) and station levels (R^2=0.49, p-value=0.022). Considering the landscape level, three landcover surface variables significantly explained species composition: %FO, %TP and %GR within a 5km buffer (**Table 4**, **Fig 8**). At the station level, species composition was explained by local habitats and landscape variables (**Table 5**). Habitat type was used as a local factor variable and explained 16% of species composition (**Table 5**, **Fig 9**). Landscape variables from each sampling station, involving forest cover and Shannon heterogeneity within a 1km buffer (FO1km and SHDI1km, respectively), and grassland within a 500m buffer (GR500m), explained 14% of species composition (**Table 5**, **Fig 9**).

Table 4. Redundancy Analysis (RDA) of variance partitioning for landscape level variables. Adjusted R2 and p-values are shown for landscape variables aggregated and separately. Significant (p<0.05) factors are highlighted in bold. References: FO5km- average percentage of forest within 5km buffer, WS7km- average percentage of wooded savanna, GR5km- average percentage of grassland within 5km buffer, TP5km- an average rate of tree plantation within 5km buffer, WA10km: water courses within 10km buffer, SHDI5km- landscape Shannon heterogeneity vector within 5km buffer.

RDA	Adj. R^2	p-value
Overall variance	**0.453**	**0.038**
SHDI5km	0.039	0.429
FO5km	**0.102**	**0.043**
GR5km	**0.099**	**0.050**
TP5km	**0.106**	**0.041**
WA10km	0.037	0.294
WS7km	0.055	0.052
Unconstrained variance	0.015	Non-testable

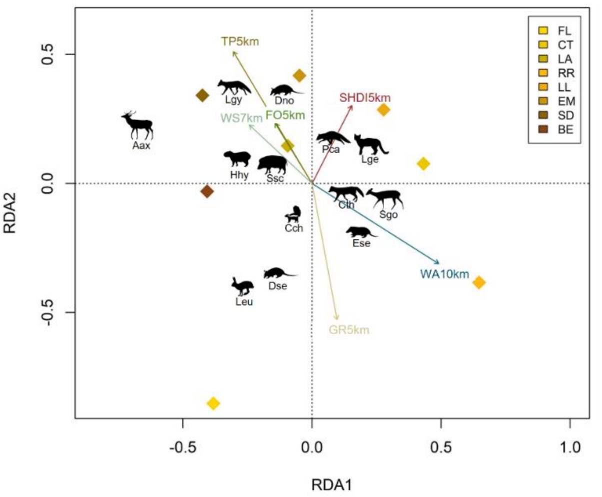

Fig 8 RDA ordination biplot of mammal species composition according to landscape level variables. Filled circles correspond to the eight studied landscapes, colored according to TP average cover (ranging from lowest to highest: FL, CT, LA, RR, LL, EM, SD, BE). Species contributions to beta-diversity with a goodness of fit ≥ 0.1 are indicated with acronyms and silhouettes -vectorized from De Angelo et al. (2017) and authors' photographs-. Species codes are shown in **Fig 5**. References: %FO: average percentage of forest, %WS: average percentage of wooded savanna, %GR: average percentage of grassland, %TP: average percentage of tree plantation, %WA: water, SHDI: landscape Shannon heterogeneity vector.

Of the 17 species, 13 contributed significantly to beta diversity through landscape and station levels (**Fig 8**, **Fig 9**). Grassland species, such as *D. septemcinctus* and *L. europaeus*, were associated with high GR cover (**Fig 8**, **Fig 9**). Forest specialists, such as *C. thous* and the gray brocket deer *Subulo gouazoubira,* were associated with increasing SHDI in FO stations. Generalist species, such as *A. axis*, the wild boar *Sus scrofa*, *D. novemcinctus,* and *L. gymnocercus,* were associated with increasing tree cover at the landscape level, considering FO, WS, and TP. Species composition within landscapes and habitat types showed no significant variation among group dispersions (compositions vary similarly with p-value=0.539 and p-value=0.362, respectively; Supplementary Material: Appendix V, Figure S10).

Table 5 Redundancy Analysis (RDA) of variance partitioning for station level variables. Adjusted R2 and p-values are shown for landscape variables aggregated and separately. Significant ($p<0.05$) factors are highlighted in bold. References: FO- forest; GR- grassland; TP- tree plantation; WS- wooded savanna; FO1km- forest cover within 1km buffer, GR500m- grassland cover within 500m buffer; TP1km- tree plantation cover within 1km buffer; WA2km: water cover within 2km buffer; SHDI2km- station Shannon heterogeneity vector within 2km buffer.

RDA	Adj. R^2	p-value
Overall variance	**0.379**	**0.022**
Habitat type (FO, WS, GR, TP)	**0.158**	**1e^{-4}**
GR500m	**0.024**	**0.038**
SHDI1km	**0.026**	**0.027**
FO1km	**0.048**	**0.008**
TP1km	0.011	0.366
WA2km	0.026	0.059
Unconstrained variance	0.086	Non-testable

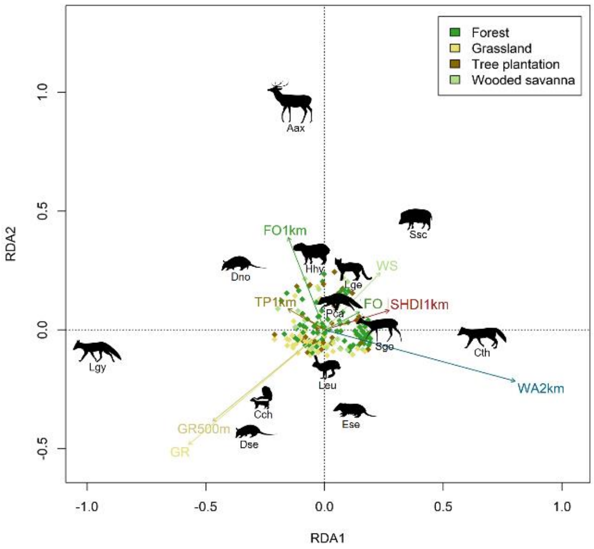

Fig 9 RDA ordination biplot of mammal species composition according to sampling station level. Filled circles correspond to camera trap stations colored according to the habitat type (FO, GR, WS, and TP). Species contributions to beta-diversity with a goodness of fit ≥ 0.1 are indicated with acronyms and silhouettes -vectorized from De Angelo et al. (2017) and authors' photographs-. Species codes are shown in **Fig 5**. References: FO- forest; GR- grassland; TP- tree plantation; WS- wooded savanna; FO1km- forest cover within 1km buffer, GR500m- grassland cover within 500m buffer; TP1km- tree plantation cover within 1km buffer; SHDI1km- station Shannon heterogeneity vector within 1km buffer; WA2km: water cover within 2km buffer.

4. Discussion

The main finding of this work was that the mammal assemblages changed according to the landscape context and remnant native habitats. TP particularly, were not "green deserts" (sensu Bremer and Farley 2010); some species are more likely to be affected by changes in landscape use and configuration, while others may easily be adapted to new habitats, be indifferent, or even be favored by it (Crooks 2002; Fischer and Lindenmayer 2007; Iezzi et al. 2021; Almeida-Maués et al. 2022).

4.1. Afforestation and landscape structure

GR cover, as expected, decreased when TP cover increased since GR is the mainly replaced ecosystem within Rio de la Plata Grasslands -RPG- (Jobbágy et al. 2006; Baldi and Paruelo 2008; Gautreau 2014; Veldman et al. 2015; Leidinger et al. 2017; Gorosábel et al. 2020). With TP, edge density -ED- increased as well. Considering the studied areas with higher ED, in the case of BE and SD, ED values are related to the increased extent of TP cover, while LL is related to the amount and size of tree stands (i.e., multiple small tree- stands). How the edge effects of TP spread into native habitats in our region is poorly known (Iezzi et al. 2019; Magioli et al. 2021; Costa et al. 2022), but several studies worldwide have demonstrated its impacts on biodiversity (Fahrig 2003; Magioli et al. 2016; Riva and Nielsen 2020). In Uruguay, there are no national regulations regarding the shape or minimum extent of the tree stands within afforested areas (Gautreau 2014); only a maximum size for tree stands was established to reduce fire risk, but not regarding native environments distribution or connectivity. Nowadays, plantation planning is being performed to achieve the highest plantation cover within the available GR areas. Considering this, management regulations regarding tree stands size and shape need to be developed, in order to minimize the negative impacts on biodiversity.

4.2. Landscape afforestation and mammal gamma diversity

Despite the wide afforestation gradient explored, from 6% to around 80%, we did not find a difference in the number of medium-large mammals inhabiting the eight landscape samples studied in the Uruguayan grassland region. But species richness alone, although extremely used, is not informative about possible changes since it is just a number (Hillebrand et al. 2018), and biodiversity not only consists of richness, but it also includes aspects of species identities and dominance. A more complete approach to describe the effects of landscape change should also include an analysis of changes in species composition (Soininen et al. 2007; Hillebrand et al. 2018). Mammal diversity was strongly influenced by changes in which species were present (i.e., identities) and their dominance (i.e., abundance). We found significant effects in species composition at the landscape level according to TP cover within a 5km buffer, but also with GR and FO cover. As the degree of afforestation of the landscape increased, reducing grassland cover, the mammal assemblages were increasingly dominated by generalist and forest species. This tendency of afforestation landscapes being dominated by habitat generalists and some forest specialist species, with almost no record of grassland specialists, was seen in other mammals studies (Martin et al. 2012; Timo et al. 2015; Brazeiro et al. 2018; Iezzi et al. 2020, 2021; Cravino and Brazeiro 2021; Almeida-Maués et al. 2022), and in other animal groups, like butterflies (da Rocha et al. 2013; Casas-Pinilla et al. 2022), ants (Martello et al. 2018), reptiles (da Rocha et al. 2013; da Silva Alves Saccol et al. 2017) and birds (Dias et al. 2013; Jacoboski et al. 2016; Phifer et al. 2017; Vaccaro et al. 2019; Jacoboski and Hartz 2020; Martínez-Lanfranco et al. 2022), but also in plants composition (Pairo et al. 2021).

Some species were exclusive of some native habitat, emphasizing the complementarity of the habitats with TP, making each landscape more heterogeneous and diverse as established in the habitat-heterogeneity hypothesis (Simpson 1949; MacArthur and Wilson 1967): more heterogeneous landscapes achieve higher diversity values. The capybara *Hydrochoerus hydrochaeris* and the lesser grison *Galictis cuja* were exclusive of native habitats, *D. septemcinctus* was recorded exclusively in GR stations, while *S. gouazoubira*, *D. albiventris*, the margay cat *Leopardus wiedii* and the neotropical river otter *Lontra longicaudis* were exclusive of FO stations. Forest specialists, such as *S. gouazoubira,* were associated with increasing SHDI related to FO stations, as seen in other regional studies (Iezzi et al. 2020).

Regarding the only specialist grassland mammal in our study region, the seven-banded armadillo (*D. septemcinctus*), reduced in abundance and frequency of occurrence along this forestation gradient. A possible tolerance threshold for this species was identified since in landscapes with less than 70% of open areas, it became less detected, and with less than 40%, they stopped being recorded.

4.3. Landscape afforestation and mammal alpha diversity

Unexpectedly, local species richness and composition varied independently from the tree-plantation cover around the sampling stations, except for species number at TP stands, which were negatively affected.

Species richness in TP stands is lower than in native habitats, especially than FO, the most diverse habitat, as was previously observed in Uruguay (Andrade-Núñez and Aide 2010; Brazeiro et al. 2018; Cravino and Brazeiro 2021; Martínez-Lanfranco et al. 2022) and in the region (Dotta and Verdade 2011; Timo et al. 2015; Iezzi et al. 2020). But the number of mammal species in TP is further reduced as TP increases in the surrounding landscape (500m buffer). These results support the idea that afforested stands support mainly sink populations of mammal species, subsidized from nearby native habitats (forests and wooded savannas). Other studies also determined that the maintenance of mammals within TP depends on natural habitat patches within the landscape, increasing landscape heterogeneity (Lindenmayer and Hobbs 2004; Fischer and Lindenmayer 2007; Lindenmayer et al. 2015; Iezzi et al. 2019).

The variability of mammal species richness and composition at the station level within native habitats were determined by the availability of native habitat in the surrounding (500m to 1km) landscape, but not by the afforestation level. The cover of native forests around the sampling stations was the main determinant of species diversity and composition in all native habitats, FO, WS and even in GR. FO are known to have an important effect on biodiversity (Tews et al. 2004) and could be acting as a source for the most mammal in these landscapes since grassland species are displaced, and therefore being identified as “keystone structures”: spatial structures providing resources or shelter essential for species (Tews et al. 2004). GR cover within the 1km buffer also positively influenced GR richness and SHDI within the 500m buffer to WS richness. Since grassland specialists are the most sensitive species in grassland afforestation (Brazeiro et al. 2018; Cravino and Brazeiro 2021), the influence of GR cover was expected. (Addicott et al. 1987; Tscharntke et al. 2012; Driscoll et al. 2013; Riva and Nielsen 2020). Landscape variables related to the scale of effect and its influence on beta diversity could be related to the dispersion ability of the species (Jackson and Fahrig 2012, 2015; Wearn et al. 2019) and were also important in other afforested landscapes (Iezzi et al. 2021).

Therefore, besides the local scale, the extent and heterogeneity of the complex mosaic of landcover types, natural and modified, were important since species processes (e.g., foraging, reproduction, movement) occur at different rates within different spatial scales.

4.4. Concluding remarks

We found that *Eucalyptus* plantation alter the landscape configuration in Uruguay reducing grasslands cover and increasing edge density. However, the community of medium to large-mammals inhabiting such landscapes with tree-plantation cover ranging from 6 to 80%, has been slightly affected so far. Since neither the smallest nor the largest radii buffers were significant in explaining mammal richness and composition patterns, the selected ranges might be a good proxy of the accurate scale of effect within the scope of observed scales, although the different species-landscape relationship may occur at scales not evaluated in this study. Species richness, both at local and landscape scales, and local species composition, varied independently from tree-plantation cover. Only in *Eucalyptus* stands, mammals richness decreased with plantation cover. Nevertheless, species composition in the landscapes was affected by the afforestation extent. Grassland specialists became less frequent as tree plantations increased across the landscape, while generalists and some forest species grew in relative abundance. Therefore, specialist grassland mammals such as the seven-banded armadillo (*D. septemcinctus*) should be the primary mammal conservation concern for the Uruguayan forestry sector.

Eucalyptus plantations maintained a portion of mammal biodiversity, integrated mainly generalists, but isolated plantations alone are not enough to support it. Native habitats in these afforested landscapes, mainly forests, wooded savannas and remanent grasslands, played a relevant role in increasing diversity and shaping local mammal communities, and therefore, they are key elements to integrate when designing such productive landscapes from a sustainability perspective.

4.5. Management recommendations

Landscape modifications and disturbance often negatively affect habitat specialist species (Futuyma and Moreno 1988; Teixeira et al. 2020), while generalist species may even benefit from temporally changing habitats as TP. The diminution of habitat specialists may lead to a homogenization of the assemblage (Martello et al. 2018; Teixeira et al. 2020; Iezzi et al. 2021; Iglesias-Carrasco et al. 2022). Different management actions may contribute to generating more heterogeneity, therefore enriching mammal assemblage (Timo et al. 2015; Iezzi et al. 2020, 2021; Teixeira et al. 2020): (1) larger spacing between trees to achieve higher understory, (2) different tree stand ages and rotational harvest schedules, (3) generating or maintaining GR and FO patches throughout the landscapes, acting as stepping stones and promoting connectivity, to fulfill the ecological requirements of specialist species. But for grassland specialist mammals, management measures considering the maintenance of higher grassland patches should be emphasized.

The possible tolerance threshold detected for grassland specialists (70-40% GR cover within a 5km radii) should be taken into consideration for national afforestation regulations and within the certification process programs for the industry (e.g., Forest Stewardship Council -FSC-, Programme for the Endorsement of Forest Certification -PEFC-). The configuration of the landscape in terms of composition and integration of natural and productive patches is key to achieving sharing/sparing connectivity landscapes.

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Competing Interest

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

A. Cravino: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation management, Writing - Original Draft, Visualization, Project administration, Funding acquisition. **J.A. Martínez-Lanfranco:** Conceptualization, Software, Formal analysis, Writing - Review & Editing, Visualization. **A. Brazeiro:** Conceptualization, Formal analysis, Investigation, Resources, Writing - Review & Editing, Visualization, Supervision.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

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Supplementary material for

Medium-large mammals across a gradient of *Eucalyptus* plantation cover within Río de la Plata Grasslands

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This file includes Appendix I-V, Tables S1-S4, and Fig S1-S10.

Appendix I – Study Area and Methods Details

Study area

Within all considered landscapes, native habitats and tree plantations were surveyed. Three native habitat types were considered: close canopy forests (referred to as forests -FO- hereafter), open canopy forests (referred to as wooded savanna -WS- hereafter), and grasslands -GR- (**Fig S1**).

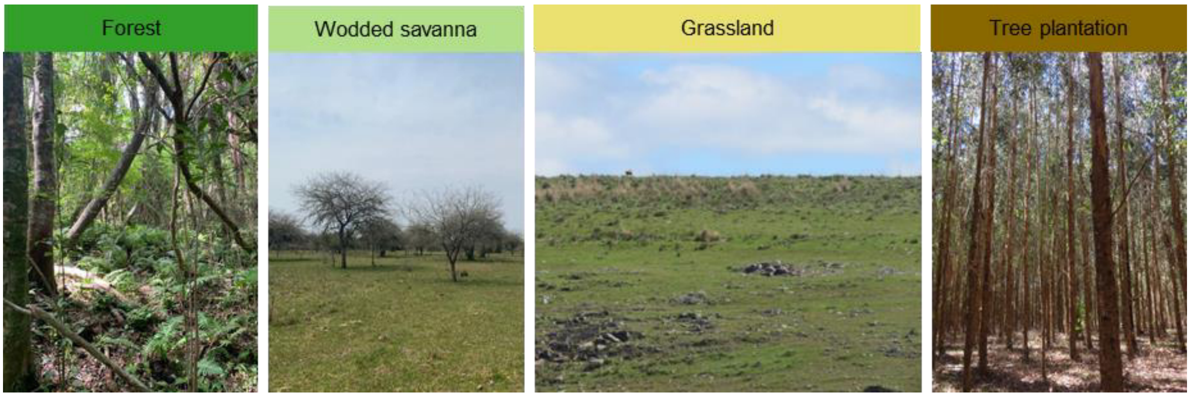


Fig S1 Illustrative photographs of habitat types surveyed.

Camera trap survey

The camera traps were active 24 hours a day throughout the sampling period and were programmed to take three 10-megapixel images upon activation by movement and temperature differences, with a high sensitivity mode and a subsequent 15-second latency. The camera model features a trigger speed of 0.5 seconds. Cameras were installed in trees or poles, facing South or North, to avoid false triggers due to direct sunlight exposure. Baits were not used, and adjacent vegetation that could activate or cover the cameras was removed to optimize detection and facilitate species recognition. The placement height was between 50 and 70cm, according to the average height of potential species, to reduce variations in detectability by body size and /or camera capture angle (Meek et al. 2016). The optimal detection distance was estimated at 3 meters from the placement site.

Appendix II – Species recorded

The regional pool of medium-large mammals in the study areas is restricted to 13 species with at least 20 records from 6 Orders and 14 Families. The complete list of species and their records is shown in **Table S1**.

Table S1 Species records according to each landscape and habitat type.

Order	**Family**	**Latin name**	**Common name**	**Ref. code**	**Landscapes**								**Habitat types**			
					FL	**CT**	**LA**	**RR**	**LL**	**EM**	**SD**	**BE**	**FO**	**WS**	**GR**	**TP**
Artiodactyla	Cervidae	*Axis axis*	Axis Deer	**Aax**	88	-	84	-	1	65	129	154	256	119	36	110
Artiodactyla	Cervidae	*Subulo gouazoubira*	Gray Brocket Deer	**Sgo**	-	38	-	12	-	-	-	-	50	-	-	-
Artiodactyla	Suidae	*Sus scrofa*	Wild Boar	**Ssc**	49	44	27	49	12	22	72	77	232	44	24	52
Carnivora	Canidae	*Cerdocyon thous*	Crab-eating Fox	**Cth**	16	22	63	140	19	8	24	33	219	51	36	19
Carnivora	Canidae	*Lycalopex gymnocercus*	Pampas fox	**Lgy**	309	227	358	20	113	138	102	109	594	147	525	110
Carnivora	Mustelidae	*Galictis cuja*	Lesser Grison	**Gcu**	-	4	6	-	-	4	-	1	11	2	2	-
Carnivora	Mustelidae	*Lontra longicaudis*	Neotropical River Otter	**Llo**	-	1	-	1	1	-	-	-	3	-	-	-
Carnivora	Felidae	*Leopardus geoffroyi*	Geoffroy's Cat	**Lge**	10	27	26	52	29	16	2	7	138	10	12	9
Carnivora	Felidae	*Leopardus wiedii*	Margay Cat	**Lwi**	-	-	1	-	-	-	-	-	1	-	-	-
Carnivora	Mephitidae	*Conepatus chinga*	Molina's Hog-nosed Skunk	**Cch**	101	29	70	13	8	18	3	25	92	9	159	7
Carnivora	Procyonidae	*Procyon cancrivorus*	Crab-eating Raccoon	**Pca**	1	8	6	29	22	7	11	7	69	5	10	7
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded Armadillo	**Dno**	118	204	120	414	73	145	62	89	811	101	181	132
Cingulata	Dasypodidae	*Dasypus septemcinctus*	Seven-banded Armadillo	**Dse**	118	-	6	1	-	-	-	-	-	-	125	-
Cingulata	Euphractidae	*Euphractus sexcinctus*	Yellow Armadillo	**Ese**	26	32	72	55	3	8	4	-	109	21	63	7
Lagomorpha	Leporidae	*Lepus europaeus*	European Hare	**Leu**	319	2	2	28	1	-	3	41	10	43	331	12
Rodentia	Caviidae	*Hydrochoerus hydrochaeris*	Capybara	**Hhy**	125	2	25	2	14	7	55	1	177	22	32	-
Didelphiomorphia	Didelphidae	*Didelphis albiventris*	White-eared Opossum	**Dal**	-	-	-	-	1	-	-	1	-	-	1	-

During surveys, 17 mammal species were recorded with the camera traps. Examples of photographs of different species captured are shown in **Fig S2**.

Axis axis
Lycalopex gymnocercus
Procyon cancrivorus
Euphractus sexcinctus
Leopardus wiedii
Leopardus geoffroyi
Lontra longicaudis
Didelphis albiventris
Sus scrofa
Conepatus chinga
Dasypus septemcinctus
Lepus europaeus
Cerdocyon thous
Galictis cuja
Dasypus novemcinctus
Hydrocherus hydrochaeris
Subulo gouazoubira

Fig S2 Species recorded on camera traps.

Appendix III – Landscapes structure

The Principal Component Analysis (PCA) allowed us to summarize and visualize the landscape information described by multiple inter-correlated quantitative vegetation structure variables from native habitats and plantations. The eigenvalues measure the variation retained by each principal component dimension; when larger than 1, it indicates that the dimension accounts for more variance than one of the single-scaled variables used. This is commonly used as a cutoff point for the dimension's retention and limiting its number to a certain fraction of the cumulative variance explained. Considering that, we selected the first two dimensions (Dim. 1 and Dim. 2) to achieve above 70% of cumulative variance and eigenvalues above one as well (**Table S2**).

Table S2 PCA dimensions eigenvalues and retained variance. Selected dimensions are shown in bold.

PCA Dimensions	Eigenvalue	Variance percent	Cumulative variance percent
Dim.1	**3.78**	**39.68**	**39.68**
Dim.2	**2.27**	**32.38**	**72.05**
Dim.3	0.44	20.40	92.45
Dim.4	0.43	6.25	98.71
Dim.5	0.05	0.78	99.49
Dim.6	0.03	0.48	99.97
Dim.7	0.00	0.03	100.00

Cos2 represents the quality of the representation of the variables. A high cos2 (closer to 1) indicates a good representation of the variable on the principal component dimension. The best representations are found on the first principal component dimension (Dim. 1) (**Table S3**). The variables with higher contributions to Dim. 1 were: GR, TP, ED, and SHDI (from 31.21 to 17.20%) (**Table S3**). For Dim. 2: FO, WS, TP, and ED (from 26.64 to 13.10%) (**Table S3**).

PCA biplots for the different buffer areas are also shown in **Fig S3**.

Table S3 Quality of representation -cos2- and variables contributions for selected dimensions. References: FO- average percentage of forest, WS- average percentage of wooded savanna, GR- average percentage of grassland, TP- average percentage of tree plantation, WA- water, ED- tree plantation edge density vector, SHDI- landscape Shannon heterogeneity vector.

Variable	Dim. 1		Dim. 2	
	cos2	Contribution	cos2	Contribution
ED	0.50	18.09	0.30	13.10
SHDI	0.48	17.20	0.23	9.99
WA	0.01	0.05	0.18	7.93
FO	0.10	3.70	0.60	26.64
TP	0.62	22.15	0.35	15.50
GR	0.87	31.21	0.05	0.23
WS	0.21	7.59	0.60	26.61

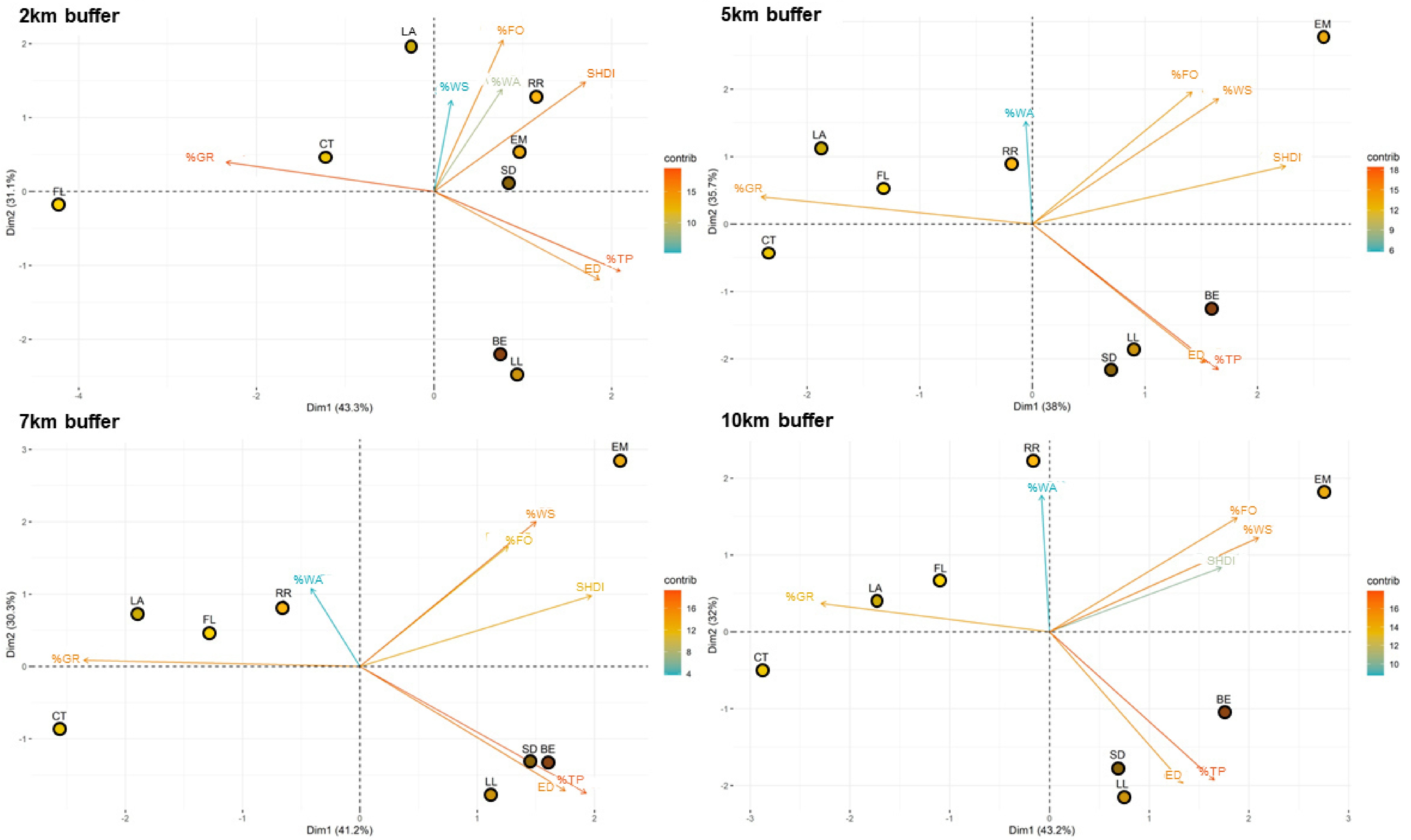


Fig S3 Biplot from principal component analyses (PCA) of landcover, heterogeneity, and tree plantation edge density from each buffer at the landscape scale (2km, 5km, 7km, and 10km). References: %FO: average percentage of forest, %WS: average percentage of wooded savanna, %GR: average percentage of grassland, %TP: average percentage of tree plantation, %WA: water, ED: tree plantation edge density vector, SHDI: landscape Shannon heterogeneity vector. The contributions of variables (contrib) are expressed in percentage and with a color gradient.

Appendix IV – Gamma Diversity (γ)

Sample coverages from the afforested landscapes were higher than 99% (**Table S4**, **Fig S4**), implying they are equally complete.

Table S4 Observed values and diversity estimations for the study landscapes (GR, CT, LA, RR, LL, EM, SD, BE) by Hill numbers of order q (^{q}D): ^{0}D, ^{1}D, and ^{2}D.

	Sample coverage (%)	Diversity	Observed value	Estimated value	Standard error
FL	100	^{0}D	12	12	0.482
		^{1}D	7.713	7.746	0.165
		^{2}D	6.251	6.277	0.195
CT	99.8	^{0}D	13	13.25	0.728
		^{1}D	5.788	5.847	0.25
		^{2}D	4.109	4.129	0.18
LA	99.8	^{0}D	14	14.499	1.322
		^{1}D	6.701	6.756	0.256
		^{2}D	4.487	4.505	0.215
RR	99.8	^{0}D	13	14.998	3.737
		^{1}D	5.245	5.293	0.215
		^{2}D	3.305	3.314	0.165
LL	99.8	^{0}D	11	11	0.143
		^{1}D	5.678	5.744	0.277
		^{2}D	4.207	4.238	0.199
EM	100	^{0}D	13	18.98	7.162
		^{1}D	6.065	6.261	0.384
		^{2}D	4.367	4.417	0.311
SD	100	^{0}D	11	11	0.478
		^{1}D	6.371	6.444	0.24
		^{2}D	5.293	5.344	0.22
BE	99.6	^{0}D	12	14.996	4.511
		^{1}D	4.393	4.438	0.182
		^{2}D	2.929	2.937	0.13

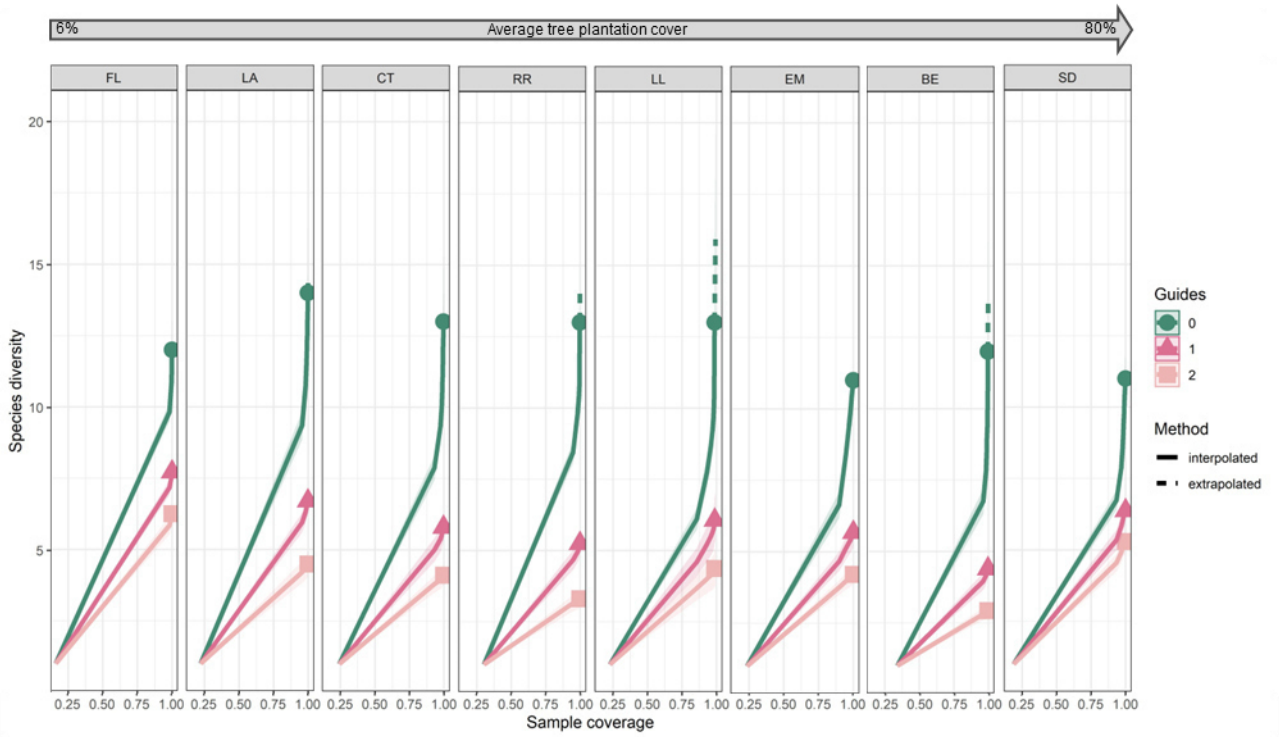


Figure S4. Coverage-based diversity rarefaction and extrapolated curves with 95% confidence intervals (color shade), showing the expected diversity ^qD as a function of the number of individuals with q = 0, 1, 2 for the study landscapes (FL, CT, LA, RR, LL, EM, SD, BE) according to tree plantation cover. Solid icons denote observed diversities in each treatment.

Considering the habitats within the landscapes separately (FO, WS, GR, and TP), the mammal diversity estimators ^0D in FO were higher than in the other habitat types. The highest values from FO were in the intermediate afforested landscapes (**Fig S5**¡Error! No se encuentra el origen de la referencia.). GR was the second most diverse habitat type, especially GR, located in grassland-dominated landscapes (**Fig S6**). The third diversity position was for WS (**Fig S7**), with no significant differences among landscapes with completely overlapped confidence intervals, followed by TP. Among landscapes, TP in the highest afforested area (BE) had significantly higher diversity (**Fig S8**).

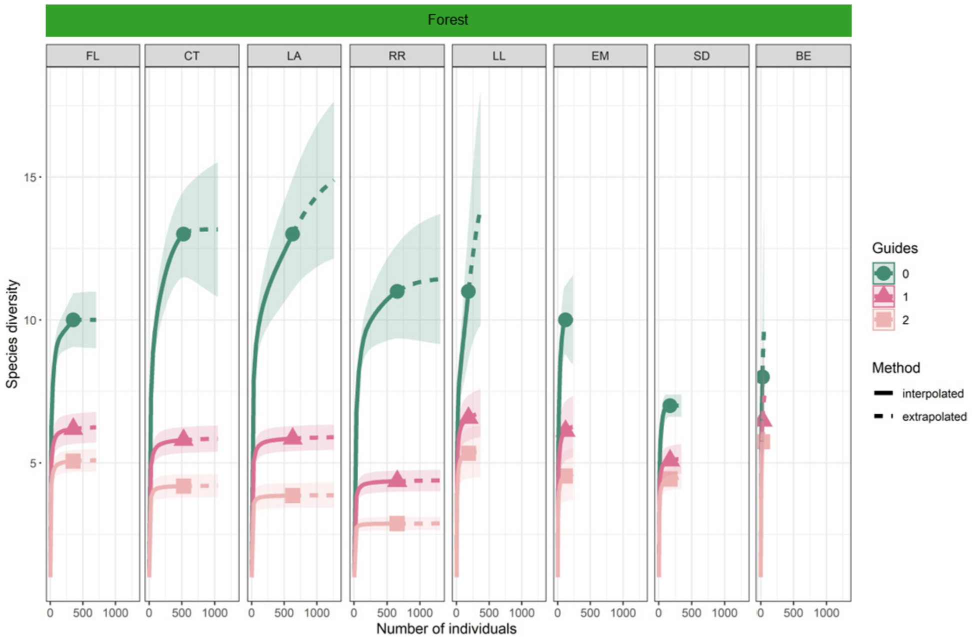


Fig S5 Sample-based diversity rarefaction and extrapolated curves with 95% confidence intervals (color shade), showing the expected diversity ${}^qD$ as a function of the number of individuals with q = 0, 1, 2 for the forests within the study landscapes (FL, CT, LA, RR, LL, EM, SD, BE) according to tree plantation cover. Solid icons denote observed diversities in each treatment.

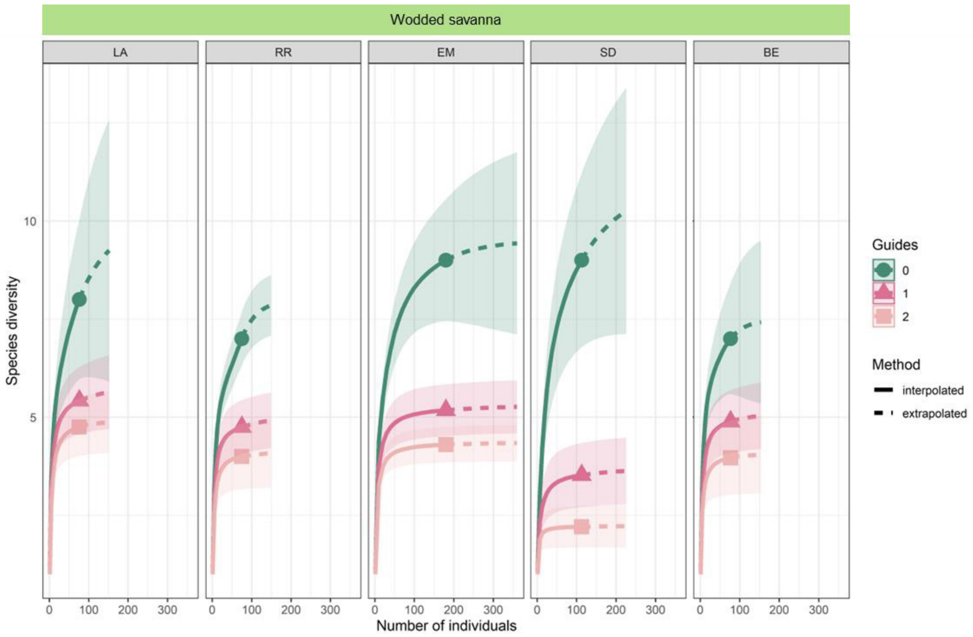


Fig S6 Sample-based diversity rarefaction and extrapolated curves with 95% confidence intervals (color shade), showing the expected diversity ${}^qD$ as a function of the number of individuals with q = 0, 1, 2 for the wooded savannas within the study landscapes (LA, RR, EM, SD, BE) according to tree plantation cover. Solid icons denote observed diversities in each treatment.

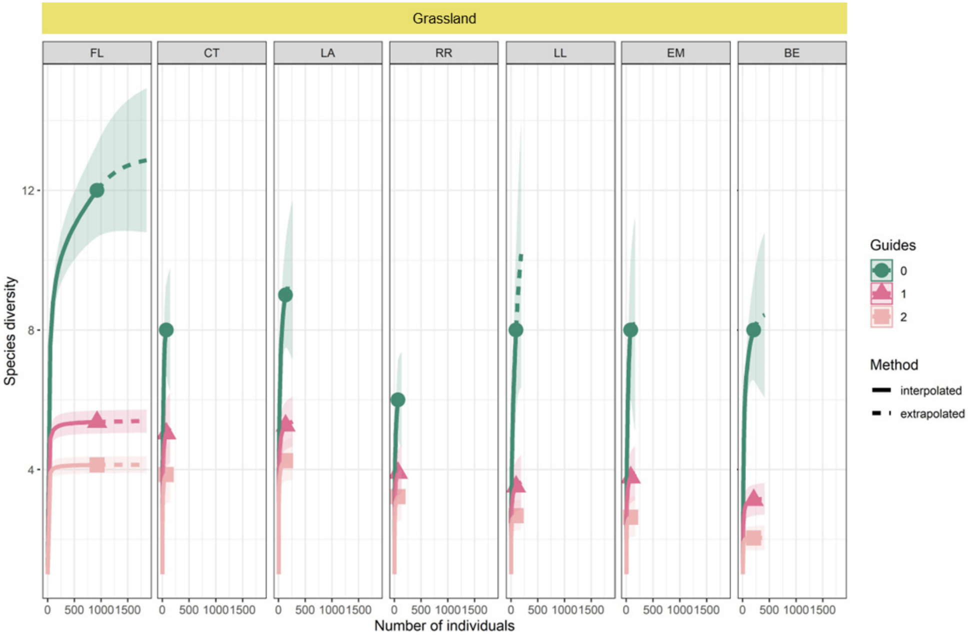


Fig S7 Sample-based diversity rarefaction and extrapolated curves with 95% confidence intervals (color shade), showing the expected diversity ${}^qD$ as a function of the number of individuals with q = 0, 1, 2 for the grasslands within the study landscapes (FL, CT, LA, RR, LL, EM, BE) according to tree plantation cover. Solid icons denote observed diversities in each treatment.

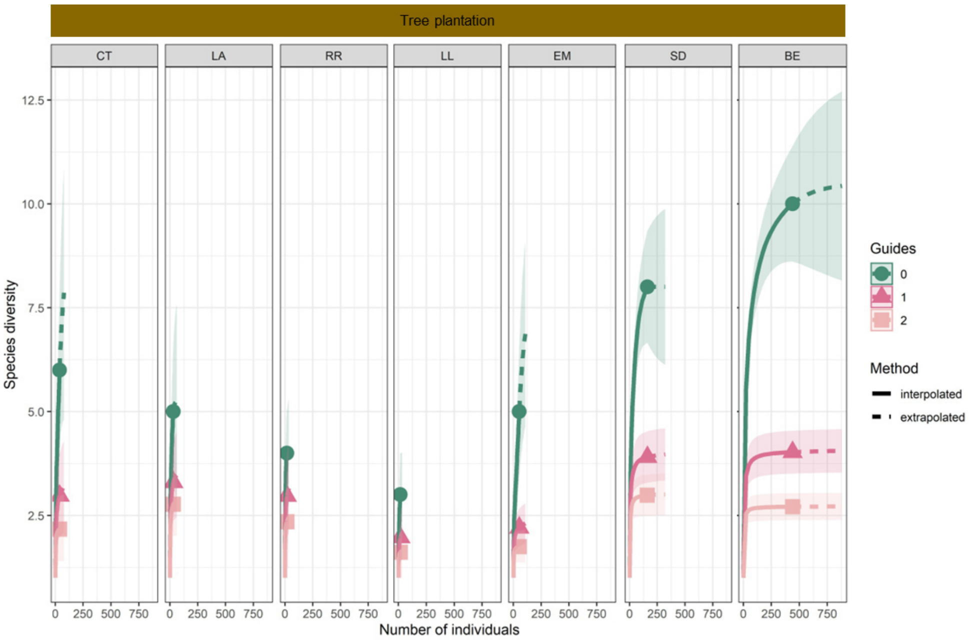


Fig S8 Sample-based diversity rarefaction and extrapolated curves with 95% confidence intervals (color shade), showing the expected diversity ${}^qD$ as a function of the number of individuals with q = 0, 1, 2 for the forests within the study landscapes (CT, LA, RR, LL, EM, SD, BE) according to tree plantation cover. Solid icons denote observed diversities in each treatment.

The species capture rate and composition varied across the different landscapes, as with the main native habitats within them (**Fig S9**).

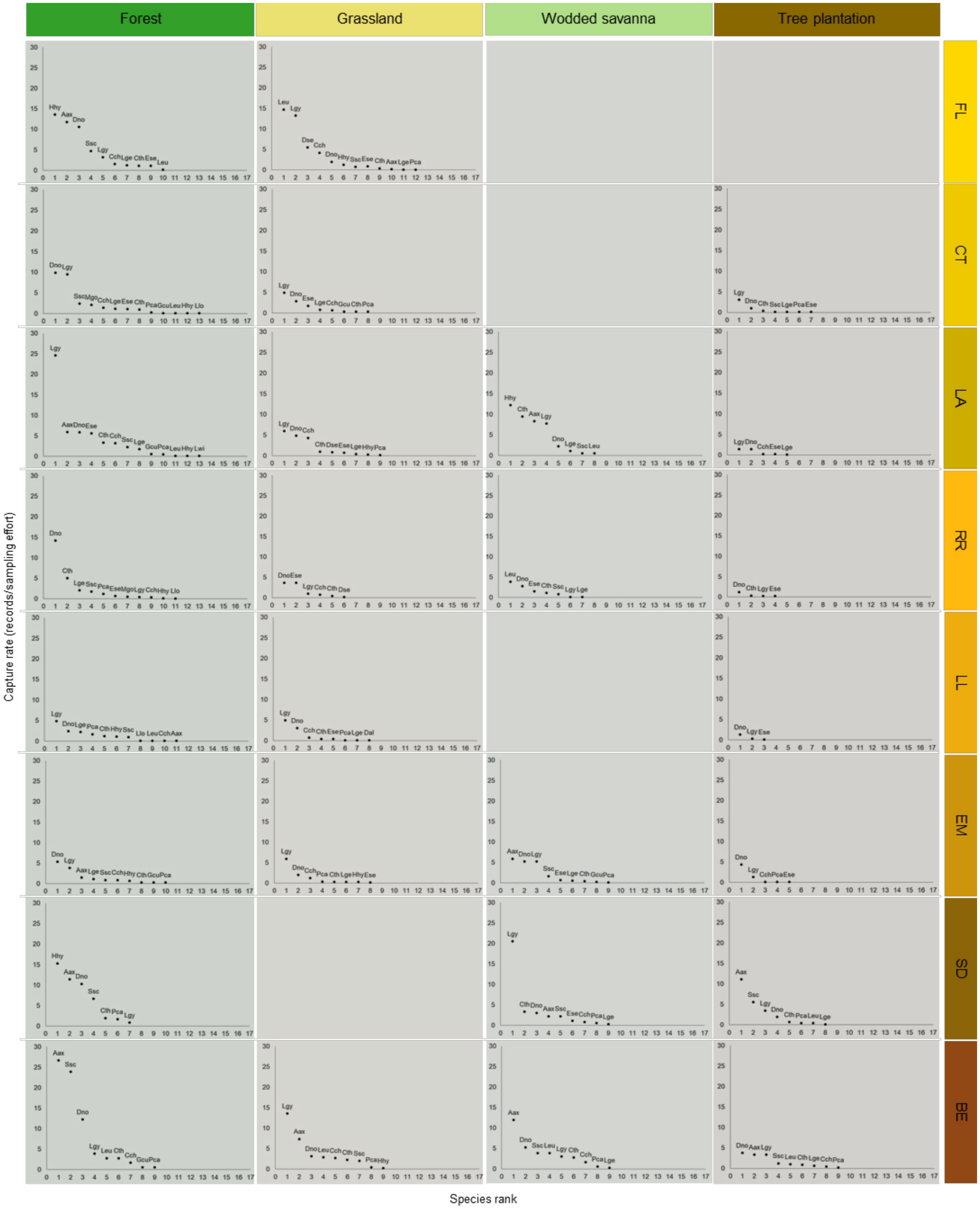


Fig S9 Rank-abundance plots for mid-large mammals detected in camera traps across habitats (forest, wooded savanna, grassland, tree plantation) within landscapes with differential plantation cover (ranging from lowest to highest: FL, CT, LA, RR, LL, EM, SD, BE). Species codes are as follow: Aax- *Axis axis*, Cch- *Conepatus chinga*, Cth- *Cerdocyon thous*, Dal- *Didelphis albiventris*, Dno- *Dasypus novemcinctus*, Dse- *Dasypus septemcinctus*, Ese- *Euphractus sexcinctus*, Gcu- *Galictis cuja*, Hhy- *Hydrocherus hydrochaeris*, Lge- *Leopardus geoffroyi*, Leu- *Lepus europaeus*, Llo- *Lontra longicaudis*, Lgy- *Lycalopex gymnocercus*, Lwi- *Leopardus wiedii*, Pca- *Procyon cancrivorus*, Ssc- *Sus scrofa*, Sgo- *Subulo gouazoubira*.

Appendix V – Beta diversity (β)

Species composition within habitat types showed no significant variation among group dispersions, as shown in **Fig S10**.

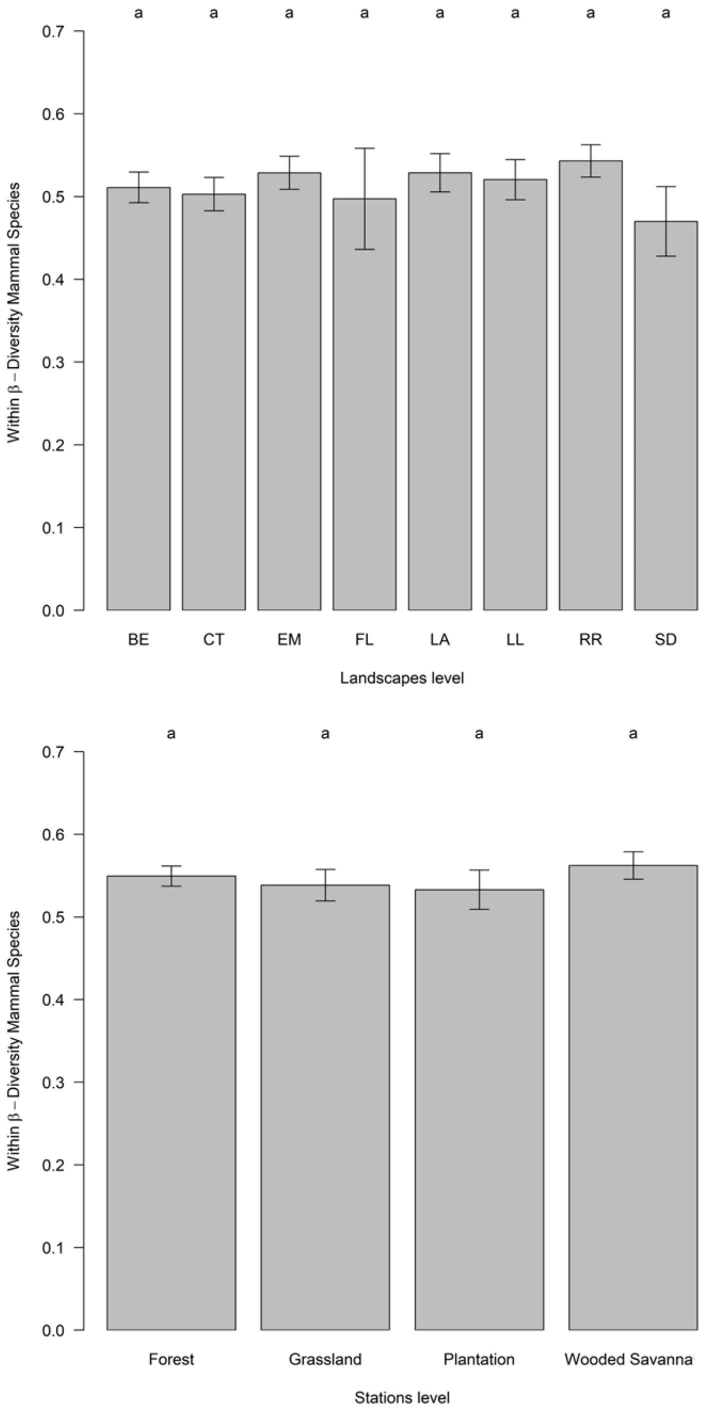
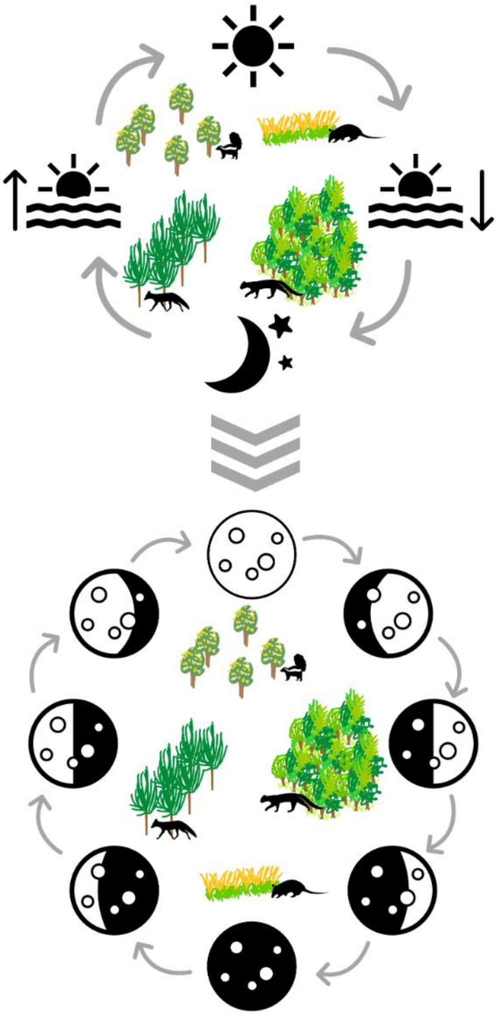


Fig S10 Beta-diversity mammal species. Bars represent mean values with standard errors. The means of habitats with the same letter are not significantly different at alpha = 0.05 using the Tukey HSD method.

References

Meek PD, Ballard GA, Falzon G (2016) The higher you go the less you will know: placing camera traps high to avoid theft will affect detection. Remote Sens Ecol Conserv 2:204–211. https://doi.org/10.1002/rse2.28

Tic, tac… dicen la luna y el sol: patrones temporales de mamíferos en paisajes con forestación de *Eucalyptus*



Tick, tock… says the moon and the sun: mammals' activity patterns in landscapes with *Eucalyptus* plantation

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Abstract

Species can change their activity patterns in response to biotic and abiotic factors. The influence of these variables is a key question for both ecological research and biodiversity conservation, considering how species adapt temporally to changing land uses and cover. The conversion of natural grasslands into tree plantations has reached outstanding levels in temperate South America. These novel ecosystems elicit behavioral changes that can either be detrimental or beneficial to wildlife, with consequences at both population and community levels. In this research, we describe the activity rhythm of mammals (mid and large-sized) during sun positions and lunar phases using camera trap data (2015-2021; 22,926 camera-nights), to assess the effects of the season (warm and cold), habitat type (native forests and grasslands, *Eucalyptus* stands and firebreaks) and landscape afforestation degree (10 to 90%) in eight landscape samples (5 km radius) at Uruguayan grasslands. This represents the first study of temporal patterns in grassland afforestation with *Eucalyptus* plantations. Across 257 camera trap stations, 5,297 independent detections of 13 species were recorded. While there were no significant differences among seasons or landscapes, habitat type affected most species temporal significant differences between native ecosystems and *Eucalyptus* plantations, despite their close spatial proximity. Cathemeral and nocturnal activity patterns were seen for 12 species, and nine showed either lunarphobic or lunarphilic trends according to habitat cover. According to tree plantation, five from seven species had narrower temporal activity than in native habitats, and four changed their nocturnality. These solar and lunar activity variations could be reactions to predation risk, hunting pressure, foraging, and competition according to habitat cover availability and to the sun and moon luminosity. With land use and land cover changes projected to continue globally, focusing research efforts on understanding species spatiotemporal responses is vital for conservation and decision making.

Key words

Grassland Afforestation, Camera traps, Habitat Type, Temporal Niche, Luminosity

Introduction

Energy is a key and finite commodity to organisms metabolism and behaviors (Brown *et al.* 2004, 2018; Boratyński 2020). The pattern of energy allocation (i.e., behavioral strategies that optimize the temporal utilization of energy) to different life behaviors (e.g., eating, resting, reproducing) over time, under environmental and physiological constraints, ultimately determines the species fitness (Daan and Aschoff 1975; Gittleman and Thompson 1988; Weathers and Sullivan 1993; Halle and Stenseth 2000; Brown *et al.* 2018). In this context, daily activity pattern is an important descriptor of animals' behavior. Activity level (the percentage of the day when animals are active) is a behavioral and ecological metric that may indicate energetic allocations of the species (Bennie *et al.* 2014; Rowcliffe *et al.* 2014), but also the environmental determinants of it (Owen-Smith 1994; Pereira 2010; Wong and Candolin 2015; Iglesias-Carrasco *et al.* 2022).

Mammals activity patterns are associated with the duration of the sunlight and/or the moonlight, which could have geographical variation (Bennie *et al.* 2014; Pratas-Santiago *et al.* 2016; Botts, Eppert, Wiegman, Blankenship, *et al.* 2020; Botts, Eppert, Wiegman, Rodriguez, *et al.* 2020). While the worldwide majority of mammals are nocturnal (69%), there also exist species with diurnal activity patterns (20%), cathemeral (8.5%), or crepuscular

(2.5%) (Bennie *et al.* 2014). But besides these general patterns, species are capable of changing their circadian activity in response to several biotic and abiotic factors, such as food acquisition, predation risk, habitat, seasonality, and luminosity (Schoener 1974; Halle 2000; Colquhoun 2006; Lucherini *et al.* 2009; Di Bitetti *et al.* 2009, 2010; Bennie *et al.* 2014; Maestri and Marinho 2014; Ordiz *et al.* 2017; Botts, Eppert, Wiegman, Blankenship, *et al.* 2020; Botts, Eppert, Wiegman, Rodriguez, *et al.* 2020; Gallo *et al.* 2022). The influence of abiotic and biotic variables on activity patterns is a key question for both ecological research and biodiversity conservation. Combining both, spatial and temporal species distribution, will help to gain valuable information about their ecological niche and for its conservation, considering how species use time, adapted to changing local conditions and habitats (MacArthur and Levins 1967; Schoener 1974; Frey *et al.* 2017).

Human-driven land use and land cover change represent a leading cause of global biodiversity loss, which has resulted in habitat loss, fragmentation, and degradation at a very rapid rate (MEA 2005; Newbold *et al.* 2015, 2016; Graham *et al.* 2019), possibly homogenizing landscapes (Wong and Candolin 2015). Besides these direct effects on biodiversity, less seen are the indirect effects of human-driven disturbances, such as species changes in behavior, like in their activity patterns (Frey *et al.* 2017; Iglesias-Carrasco *et al.* 2022). The conversion of natural grasslands into crops and tree plantations, has reached outstanding levels in temperate South America, especially in the Río de la Plata Grasslands (RPG) (Jobbágy *et al.* 2006; Baldi and Paruelo 2008; Gautreau 2014; Veldman *et al.* 2015; Leidinger *et al.* 2017; Gorosábel *et al.* 2020). Uruguay, fully immersed within the RPG (Soriano 1991; Paruelo *et al.* 2007), has experienced a strong expansion of grassland afforestation (*Eucalyptus* and *Pinus*).

Forestry creates novel environments that can threaten wildlife by disrupting ecologically relevant behaviors that are essential to their reproduction and survival (Iglesias-Carrasco *et al.* 2022). However, this novel and contrasting environment in grasslands dominated landscapes could also elicit behavioral changes with beneficial effects on the survival and reproduction of some species, as generalists or forest specialists. Anthropic environmental changes influence species interactions by altering species spatial and temporal distribution and how they overlapped (Wong and Candolin 2015). It is well known that afforestation affects mammals habitat-use (intensity and richness) in grassland-dominated landscapes (Dotta and Verdade 2011; Lantschner 2012; Timo *et al.* 2015; Veldman *et al.* 2015; Iezzi *et al.* 2020, 2021; Cravino and Brazeiro 2021), but studies about the effects on daily activity patterns and temporal niche are still missing.

Eucalyptus plantations differ structurally from the natural grasslands they replace (Cravino and Brazeiro 2021; Cravino *et al.* submitted). Such drastic habitat alterations are surely associated with changes in microclimate, frequencies, and identities of prey and predators, and essential resources (e.g., food, roosting sites). Besides, human presence increases in *Eucalyptus* plantations (Iglesias-Carrasco *et al.* 2022; Cravino *et al.* submitted). These alterations could induce behavioral adjustments in mammals, with either detrimental or beneficial impacts on species survival and reproduction and so with possible consequences on populations and communities.

Considering this, we address two main questions in this study: (1) do mammals adjust their activity patterns in *Eucalyptus* plantations with respect to natural habitats? (2) do mammals adjust their activity patterns in natural-habitats patches (grasslands, forests) as *Eucalyptus* plantation cover increases in landscapes where they are immersed?

Research on mammal activity patterns is usually arranged with a clock on a 24-h time period ("clock-time") (Frey *et al.* 2017; Caravaggi *et al.* 2017, 2018). But the sun position at the same "clock-time" ("sun-time"), changes almost every day throughout the year in northern and southern latitudes (Nouvellet *et al.* 2012; Bennie *et al.* 2014; Rowcliffe *et al.* 2014; Vazquez *et al.* 2019; Botts, Eppert, Wiegman, Rodriguez, *et al.* 2020), affecting sunset and sunrise time, and so day length. During nighttime, there is seasonal and latitudinal variation in the duration of moonlight, according to the lunar cycle, cloud cover, and topography (Bennie *et al.* 2014; Frey *et al.* 2017; Botts, Eppert, Wiegman, Blankenship, *et al.* 2020).

Thus, we analyze the activity rhythm of medium-large mammals according to sun positions and lunar phases using camera traps to assess the effects of the season, the local habitat type (native habitats *vs* *Eucalyptus* plantations), and the landscape afforestation degree, in grassland-dominated landscapes of Uruguay.

Methods

Study areas

Uruguay, located in the southeast of South America (30°05′08″-34°58′27″ S, 53°10′58″-58°26′01″ W), has a continental area of 176,215 km². The climate is classified as Humid subtropical -or temperate *sensu* INUMET (INUMET 2020)-, type "Cfa" *sensu* Köppen-Geiger- (Köppen and Geiger 1926; Beck *et al.* 2018). According to the official land-cover map of 2015, natural grasslands represent the dominant ecosystem (~60%) in the Uruguayan landscape, with native forests representing 4.8% and other native ecosystems (e.g., wetlands, shrublands) less than 1% (MVOTMA-DINOT 2015). The most widespread productive activity is cattle ranching, mainly in grasslands (natural and semi-natural), but also in forests, savannas, and some wetlands (DIEA-MGAP 2019). Among anthropic covers, croplands (including artificial grasslands) represent 27.5% of the territory, afforestation 7.9%, and urban and other artificial areas about 0.8% (MVOTMA 2012).

This study was conducted in one of the main afforested regions of Uruguay, on the Midwest side of the country (**Fig. 1**). Within this region, eight study areas were grouped into six landscape types according to the percentage of tree plantation cover -TPC- within circles of 5km radii: up to 10% ($TPC \leq 10\%$), up to 25% ($10\% < TPC \geq 25\%$), up to 40% ($25\% < TPC \geq 40\%$), up to 65% ($40\% < TPC \geq 65\%$), up to 80% ($65\% < TPC \geq 80\%$) and up to 100% ($80\% < TPC \geq 100\%$). TPC was measured in 1:5000 landcover maps.

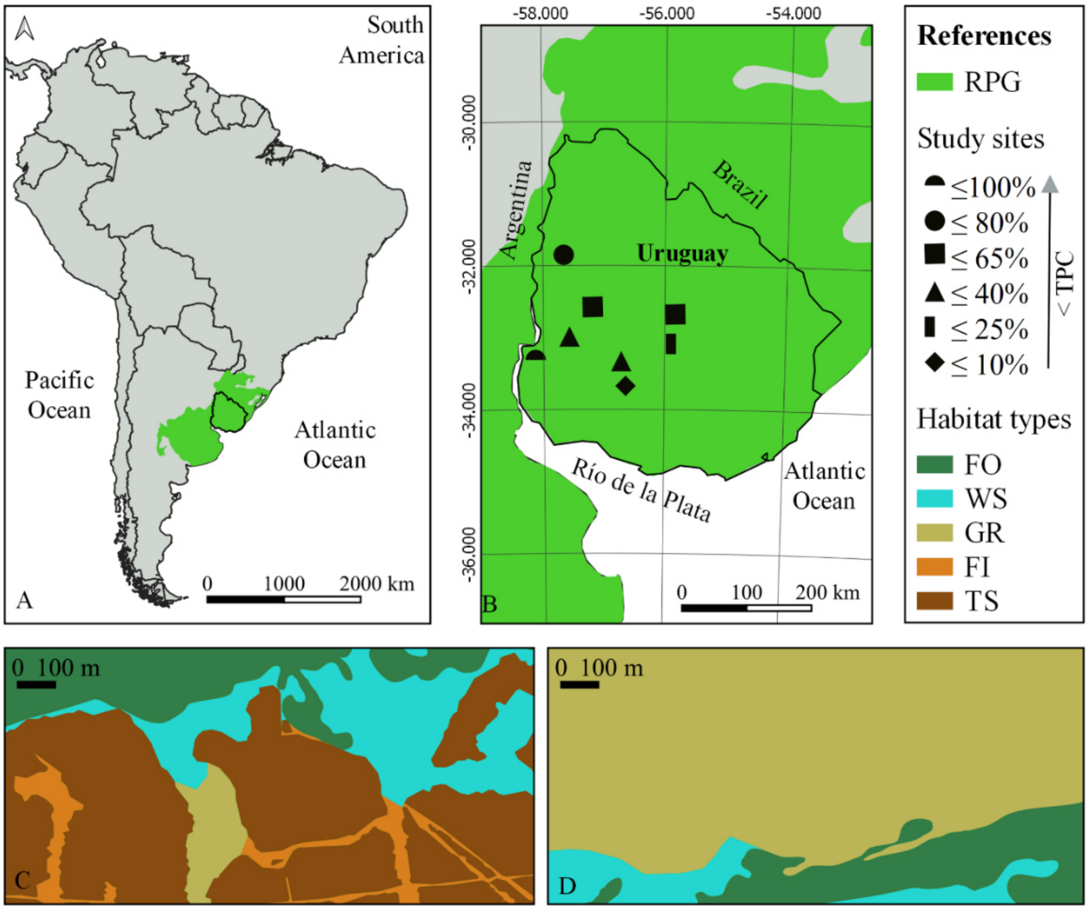

Fig. 1 Study areas. A) Río de la Plata Grassland (RPG); B) Study sites according to tree plantation cover (TPC): ≤10, ≤25, ≤40, ≤6,5, ≤80, and ≤100%. C) Landcover example of ≤100% TPC; D) Landcover example of ≤10% TPC. Habitat types are shown: Firebreak (FI), Tree Stand (TS), Forest (FO), Wooded Savanna (WS), and Grassland (GR).

Within each landscape, four habitat types were surveyed when present: tree plantation (TP), Forest (FO), Wooded Savanna (WS) and Grassland (GR). Within TP, two main components were considered, Firebreak (FI) and Tree Plantation Stand (TS); FI are uncultivated linear strips (4-8 m) with herbaceous cover located between TS, that are part of the forestry planning and are legally defined in Uruguay. Monitored FO were characterized by high values of tree density and canopy cover, while WS had lower values and therefore more distance between trees. More information on habitat types could be found in the Supplementary Material (Appendix I, Fig. S1).

Sampling design and mammal survey

The sampling design was established to compare the differences in activity patterns of the medium and large-sized mammals between the five habitat types (FI, TS, FO, WS, and GR) within the six landscapes (≤10, ≤25, ≤40, ≤65, ≤80, and ≤100%). In those categories, camera traps -CT- (Stealth Cam G42NG) were installed in 257 sampling stations between 2015 and 2021 (**Table 1**).

Table 1. Sampling effort and camera trap stations among landscapes, classified according to tree plantation cover (TPC) category (named by upper boundaries) and habitat types. Sampling effort is expressed as active camera nights. Acronyms of habitat types are: firebreak -FI-, tree plantation stand -TS-, native forest -FO-, wooded savanna -WS- and grassland -GR-.

TPC (%)	Survey Dates	Sampling Effort	Camera Trap Stations				
			FO	WS	GR	TS	FI
≤10	2020-2021	2837	8	-	12	-	-
≤25	2015-2016	3348	20	-	7	5	5
≤40	2015-2016	5833	22	12	17	10	10
≤65	2016-2017	6052	32	8	19	10	10
≤80	2019-2020	2110	8	4	-	8	8
≤100	2020-2021	2746	3	4	5	5	5

Sampling stations had a single CT established following a stratified random sampling design by habitat type at each landscape for a year long. CT were arranged with a separation of 0.5 km to 1 km (mean distance = 0.71 km, min=0.58 km, max=7.45 km), trying to reduce the probability of detecting the same individuals in different cameras (i.e., independence between stations) and at the same time optimizing the area to be covered. Stations not been autocorrelated was also confirmed with the Moran's Index (p-value>0.05) in the ape R package (Paradis and Schliep 2019; Kolowski *et al.* 2021). The mapping, selection, and placement of sampling points were performed using QGIS 2.14.15 (QGIS Development Team 2022). More details about camera traps set up and installation are shown in the Supplementary Material (Appendix I, Fig. S2).

Data processing

Exifpro image management software (Kowalski 2013) was used for image processing, tagging species and extracting pictures metadata. The analysis was continued with the camtrapR package (Niedballa *et al.* 2016) in the statistical software R (R Core Team 2022).

To avoid multiple counting of the same individual at a sampling station for a brief period, all images of the same species taken over one hour were considered an independent event. The one-hour span was considered adequate in similar camera trap studies for medium-large mammals (Lantschner 2012; Decarre 2015; Cravino and Brazeiro 2021). Livestock was not considered in subsequent analyses.

Statistical analysis

Each independent record was defined as an activity event, considering that camera traps capture animals in movement, therefore in active periods, and assuming that species capture rate at a given time of day is proportional to the activity level of the population at that time (Rowcliffe *et al.* 2014). The species with at least 20 independent records per habitat type in each landscape were considered for all activity patterns analysis. Mammals´ records at both afforestation components, FI and TS, showed the same temporal pattern, and therefore they were analyzed together as TP.

Besides activity budgets -*when species are active over the day*-, the activity pattern of each species was described generally by two separate measurements: activity level (Act)- (Rowcliffe *et al.* 2014) and percent of nocturnal activity (%Night). Act refers to *how much the species are active over the full day* (Rowcliffe *et al.* 2014), ranging from 0 to 1 within a 24h cycle; measurements were performed with the activity R package (Rowcliffe 2022).

Sun´s position according to local time and space were obtained with the suncalc R package (Thieurmel and Elmarhraoui 2019). Four sun-time stages were considered: (1) Sunrise Start (SRS), (2) Sunrise End or Dawn (SRE), (3) Sunset Start (SSS), and (4) Sunset End or Dusk (SSE). Definitions of these sun position stages and their usage for this research are shown in the Supplementary Material (Appendix I, Table S1). Species records between SRE and SSS were categorized as daytime records, while records between SSE and SRS were considered nighttime records. Finally, records between SSS and SSE, and between SRS and SRE, were considered as twilight or crepuscular records. These classifications were used for the %Night calculations -*how much of the species activities occurred at night*- (i.e., percentage of records between SSE and SRS).

We first checked if there were no statistical differences for “Act” and “% Night” between seasons (Warm, Cold). The Warm season was defined between September 21st and March 20th, covering spring and summertime. The Cold season was defined between March 21st and September 20th, covering fall and wintertime. Since no differences were found, all records were gathered.

To assess the effects of local habitat types (TP, FO, WS, GS) and landscapes with different TPC categories (≤10, ≤25, ≤40, ≤6,5, ≤80, and ≤10,0%), we fit a General Linear Mixed Model (GLMM) with binomial distribution (logit function). Landscapes were included as fixed effects and local habitat type was nested within them as interactions, with species as a random effect to control for species-specific differences; interaction models were also performed for single species. The sampling effort varied, so we included it in logarithmic scale as an offset term in the models. Since no significant interactions were found for landscapes and habitats, we used a simple one-factor analysis to evaluate differences among habitats, pooling the landscapes complete dataset. When significant differences were found among habitats, Mann-Whitney post-hoc tests were performed, also called Wilcoxon's range test (Quinn and Keough 2002). Significance analyzes were accomplished with the stats (R Core Team 2022) and car (Fox and Weisberg 2019) R packages. The models and further assessments were performed with the R packages glmmTMB (Brooks *et al.* 2017), DHARMa (Harting 2022), effects (Fox and Weisberg 2019, 2018), sjPlot (Lüdecke 2021), MuMIn (Barton 2022), and emmeans (Lenth 2022).

Species solar activity patterns

For characterizing the activity budgets of the surveyed species, records were cataloged according to the sun position stages (sun-time) (Nouvellet *et al.* 2012; Vazquez *et al.* 2019) with the overlap R package (Ridout and Linkie 2009). Solar positions were scaled to radians so that 0 (zero) corresponds to midnight, $3\pi/2$ to sunset, $\pi/2$ to sunrise, and π to solar noon.

Species were assigned to one of six activity patterns categories adapted from Azevedo et al. (2018): (1) nocturnal -active only at night- (≥90% of records at night); (2) mostly nocturnal (70-89% of records at night and twilight); (3) crepuscular -active mainly during twilight- (≥80% of records around sunrise and sunset); (5) cathemeral (Tattersall 1987) -active throughout the day and night- (30-69% of records at night and twilight); (5) diurnal -active only during the day-; and (6) mostly diurnal (10-29% of records at night and twilight).

Circular activity budgets were performed considering sun-time for each habitat type where the species had more than 20 independent events with the circular and activity R package (Rowcliffe 2022). Nonparametric circular kernel density estimations to times of animal captures and plots were made with the NPCirc (Oliveira *et al.* 2014) and circular R packages (Agostinelli and Lund 2022). The Watson's Test for circular uniformity (WT) was used to determine whether the species activity patterns differed significantly from what would be expected by chance, within each habitat type. The test was performed in the circular R package (Agostinelli and Lund 2022). Probabilities below the significance level (p-value<0.05) indicate that species activity patterns were not distributed uniformly and showed evidence of an activity trend.

The overlap coefficient (Δ) between each habitat type was estimated using the R package overlap (Ridout and Linkie 2009). The Δ measures the similarity between two circular density curves, ranging from 0 (no overlap) to 1 (complete overlap). Dhat1 (Δ1) was used when the sample size was small (>20 and ≤75 independent records) and Dhat4 (Δ4) for large samples (>75) (Ridout and Linkie 2009). Since Δ is a descriptive measure of overlap, without indications of significant differences, the Mardia-Watson-Wheeler Test -MWW- (Jammalamadaka and SenGupta 2001) was performed using the circular R package (Agostinelli and Lund 2022).

Species lunar activity patterns

Night records (records between SSE and SRS) that occurred when the moon altitude -MA- was above the horizon (between moonrise -MRI- and moonset -MSE-) and without full cloud cover -CC- (CC<60%), were used for analyzing the lunar activity patterns across habitat types; species with at least 20 independent night records were included. CC was obtained considering the place and time of the records with the RNCEP R package (Kemp *et al.* 2012) from data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (http://www.esrl.noaa.gov/psd/). Lunar phases, MA, MRI and MSE times were obtained with the suncalc R package (Thieurmel and Elmarhraoui 2019). Definitions of these lunar stages and their usage are shown in the Supplementary Material (Appendix I, Table S1). Moon phases were scaled to radians so that 0 (zero) corresponds to New Moon, $\pi/2$ as First Quarter, π as Full Moon, and $3\pi/2$ as Last Quarter. The lunar activity patterns of each species by habitat types were fitted with non-parametrical kernel density functions in the overlap R package (Ridout and Linkie 2009). Species were classified as "lunarphobic" when showed nocturnal activity peaks during new moon (≤30% of the records on full moon), and "lunarphilic" when peaks were found during full moon (≥30% of the records on full moon) (Botts, Eppert, Wiegman, Blankenship, *et al.* 2020). When day records were enough, night and day activity according to the moon phases was analyzed for each species and habitat type (Supplementary material: Appendix IV). Same as for solar patterns, the WT was performed to check if the species activities along moon phases were significantly different from what would be expected by chance within each habitat type. The lunar activity overlap coefficient (Δ) between habitat types was calculated with the overlap R package (Ridout and Linkie 2009), and the MWW was performed with the circular R package (Agostinelli and Lund 2022).

Results

A total of 5,297 independent detections of 13 species -with at least 20 records each- were recorded across 257 camera trap stations with a sampling effort of 22,926 camera-nights (**Table 1**). Two species had more than 1,000 records: the nine-banded armadillo (*Dasypus novemcinctus*, Family: Dasypodidae) and the pampas fox (*Lycalopex gymnocercus*, Family: Canidae); four species between 500 and 300: the European hare (*Lepus europaeus*, Family: Leporidae), the axis deer (*Axis axis*, Family: Cervidae), the crab-eating fox (*Cerdocyon thous*, Family: Canidae) and the Molina´s hog-nosed skunk (*Conepatus chinga*, Family: Mephitidae); five species between 300 and 100: the wild boar (*Sus scrofa*, Family: Suidae), the capybara (*Hydrochoerus hydrochaeris*, Family: Cavidae), the Geoffroy´s cat (*Leopardus geoffroyi*, Family: Felidae), the yellow armadillo (*Euphractus sexcinctus*, Family: Euphractidae) and the seven-banded armadillo (*Dasypus septemcinctus*, Family: Dasypodidae); and two species with less than 100 records: the crab-eating raccoon (*Procyon cancrivorus,* Family: Procyonidae) and the grey brocket deer (*Subulo gouazoubira*, Family: Cervidae).

FO was the richest habitat with 11 species recorded, followed by WS and GR with nine species, and TP with six. Within TP components, FI had higher species richness (10) and number of records (543) than TS (six species, 69 records). *D. septemcinctus* was recorded only on GR of the grassland dominated landscape (TPC≤10%). *L. geoffroyi*, *S. gouazoubira* and *P. cancrivorus* had more than 20 records only on forest habitats in several landscapes. For those species, no comparisons were made. More details on species records are shown in the Supplementary Material (Appendix II, Table S2).

There were no significant differences among species activity level (Act) or night records (%Night) considering seasons and no significant interactions between landscapes and habitats according to GLMMs (**Fig. 2**; Supplementary Material: Appendix III, Table S3, Fig. S3 and S4). According to habitat types, there were significant differences for 7 of 9 species registered in more than one habitat (**Fig. 3**; Supplementary Material: Appendix III, Tables S3 and S4). Cathemeral and nocturnal activity patterns were seen for 13 species. According to TP, from the seven species with enough records, five had narrower temporal activity than in native habitats and four changed their nocturnality patterns (2 reductions and 2 increases).

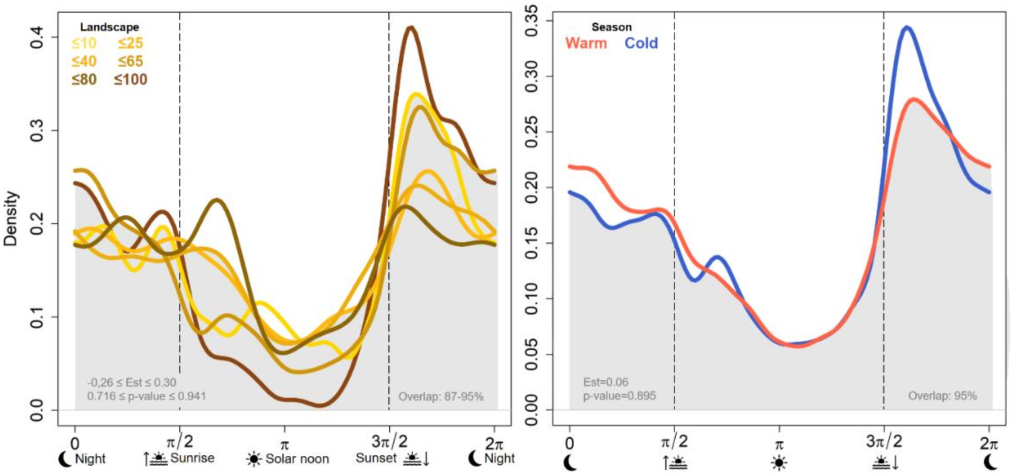

Fig. 2 General activity pattern with overlapping coefficients according to landscapes with differential tree plantation cover (≤10, ≤25, ≤40, ≤65, ≤80, and ≤100% TPC) and seasons (Warm and Cold). Estimates and p-values of GLMM are shown. Colors represent different landscapes and seasons, and overlapped sections are shown in grey shade. Note the different values on Y-axis.

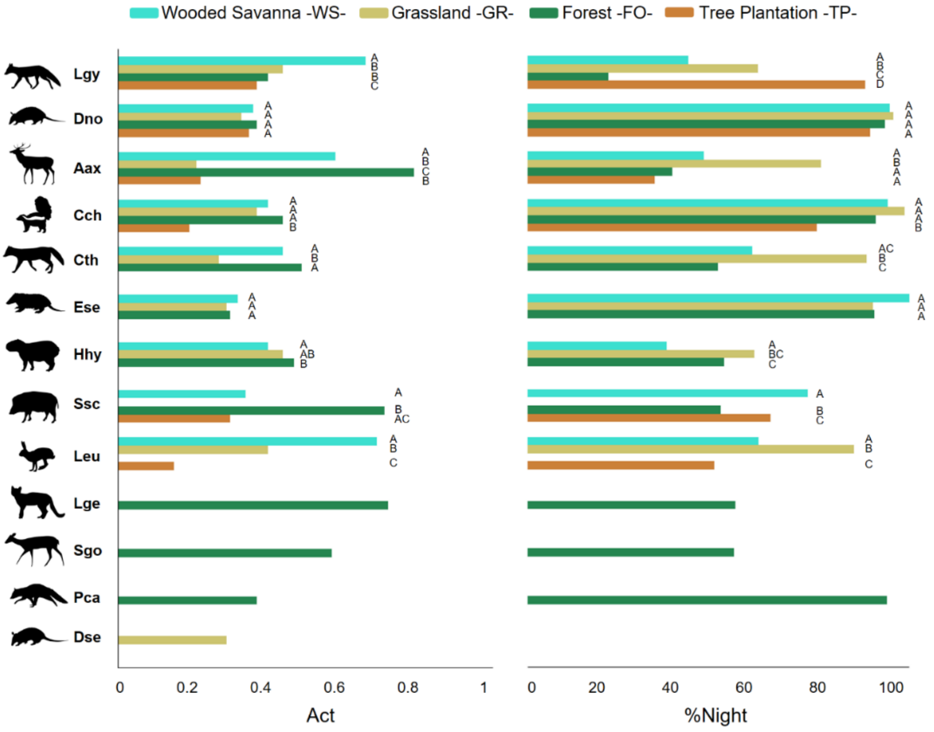

Fig. 3 Species activity level (Act) and percent of night records (%Night) according to habitat type. Mann-Whitney p-values that were significantly different between habitat pairs (FO, WS, GR, TP) are shown with different letters. Species are identified by acronyms and silhouettes -vectorized from (De Angelo et al. 2017) and authors photographs-. References: Aax- *Axis axis*; Cth- *Cerdocyon thous*; Cch- *Conepatus chinga*; Dno- *Dasypus novemcinctus*; Dse- *Dasypus septemcinctus*; Ese- *Euphractus sexcinctus*; Hhy- *Hydrochoerus hydrochaeris*; Leu- *Lepus europaeus*; Lge- *Leopardus geoffroyi*; Lgy- *Lycalopex gymnocercus*; Pca- *Procyon cancrivorus*; Sgo- *Subulo gouazoubira*; Ssc- *Sus scrofa*.

Species solar activity patterns

Differences among habitat types were not only found in Act, but also in %Night, and therefore in their circadian activity patterns (**Table 2**, **Fig. 3**; Supplementary Material: Appendix III, Table S4).

Among the species recorded in all habitat types, *D. novemcinctus* was the only one that showed no significant differences considering Act, %Night or circular pattern (**Table 2**, **Fig. 3**, **Fig. 4**). Records were not uniformly distributed throughout the day (FO: WT=17.3, p-value<0.01, GR: WT=4.44, p-value<0.01, WS: WT=1.61, p-value<0.01, TP: WT=1.79, p-value<0.01) and showed a nocturnal pattern in all habitats (**Fig. 3**, **Fig. 4**). For the opposite, *L. gymnocercus* showed significant differences in all habitat pairs (**Table 2**, **Fig. 3**, **Fig. 4**; Supplementary Material: Appendix III, Table S4). Circadian activity had no uniform pattern in FO (WT= 3.56, p-value<0.01), GR (WT=3.12, p-value<0.01), and TP (WT=5.40, p-value<0.01), while a uniform pattern was registered in WS (WT=0.09, p-value>0.1), showing cathemeral activity in that habitat type. Within TP the activity was nocturnal, in GR mostly nocturnal, while in FO it was diurnal; records overlapping vary from 37% to 81% between habitats (**Table 2**, **Fig. 3**, **Fig. 4**). *A. axis* showed no uniform pattern in GR (WT=0.74, p-value<0.01), WS (WT=0.45, p-value<0.01) and TP (WT=0.51, p-value<0.01), while an almost uniform pattern was found in FO (WT=0.23, p-value<0.05). Significance differences were detected between all habitat comparisons (**Table 2**, **Fig. 3**). The activity patterns overlapped from 46% to 80% (**Table 2**, **Fig. 3**, **Fig. 4**). Cathemeral activity was seen in FO, WS, and TP, but activity levels differed (**Fig. 3**, **Fig. 4**); in FO the activity showed constant movement during all sun positions, followed by WS, while in TP three isolated peaks were found (**Fig. 4**) and in GR, the activity was mostly nocturnal. For *C. chinga*, circadian activity showed no uniform pattern across the daily solar cycle in all habitats (FO: WT=1.68, p-value<0.01, GR: WT=3.46, p-value<0.01, WS: WT=0.98, p-value<0.01, TP: WT=0.89, p-value<0.01). In native habitat types there were no significant differences and a constant nocturnal pattern (**Table 2**, **Fig. 3**, **Fig. 4**). No significant differences were found in contrast to all native habitats in circular activity pattern, Act and %Night (**Table 2**, **Fig. 3**), and records were mostly nocturnal, with dispersed encounters (**Fig. 4**).

Table 2. Between habitat pairs comparison of species daily activity patterns (Forest -FO-, Wooded Savanna -WS-, Grassland-GR-, Firebreak -FI-). Values shown represent: species-habitat daily activity overlap value (Δ) and Mardia-Watson-Wheeler p-values for circular patterns comparisons (MWW). Significant p-values (<0.05) are shown in bold. Species are identified by acronyms and silhouettes -vectorized from (De Angelo et al. 2017) and authors photographs-. References: Aax- *Axis axis*; Cth- *Cerdocyon thous*; Cch- *Conepatus chinga*; Dno- *Dasypus novemcinctus*; Ese- *Euphractus sexcinctus*; Hhy- *Hydrochoerus hydrochaeris*, Leu- *Lepus europaeus*; Lgy- *Lycalopex gymnocercus*; Ssc- *Sus scrofa*.

Habitat types		**Species daily activity patterns differences**								
		Aax	***Cth***	***Cch***	***Dno***	***Ese***	***Hhy***	***Leu***	***Lgy***	***Ssc***
GR-FO	Δ	0.469	0.622	0.835	0.900	0.822	0.786	-	0.622	-
	MWW	**1e-06**	**6e-03**	0.799	0.119	0.389	0.363	-	**2e-16**	-
GR-WS	Δ	0.486	0.676	0.806	0.843	0.714	0.694	0.736	0.812	-
	MWW	**1e-04**	**0.024**	0.145	0.040	0.311	0.072	**0.002**	**8e-05**	-
GR-FI	Δ	0.463	-	0.511	0.823	-	-	0.533	0.743	-
	MWW	**3e-05**	-	**5e-06**	0.129	-	-	**3e-09**	**6e-12**	-
FO-WS	Δ	0.809	0.783	0.806	0.887	0.749	0.655	-	0.757	0.719
	MWW	**0.021**	0.155	0.177	0.333	0.392	0.158	-	**3e-06**	**0.025**
FO-FI	Δ	0.578	-	0.582	0.848	-	-	-	0.368	0.556
	MWW	0.296	-	**0.001**	0.115	-	-	-	**2e-16**	**0.008**
WS-FI	Δ	0.604	-	0.446	0.804	-	-	0.525	0.592	0.528
	MWW	**0.033**	-	**2e-05**	0.059	-	-	0.176	**2e-15**	**0.019**

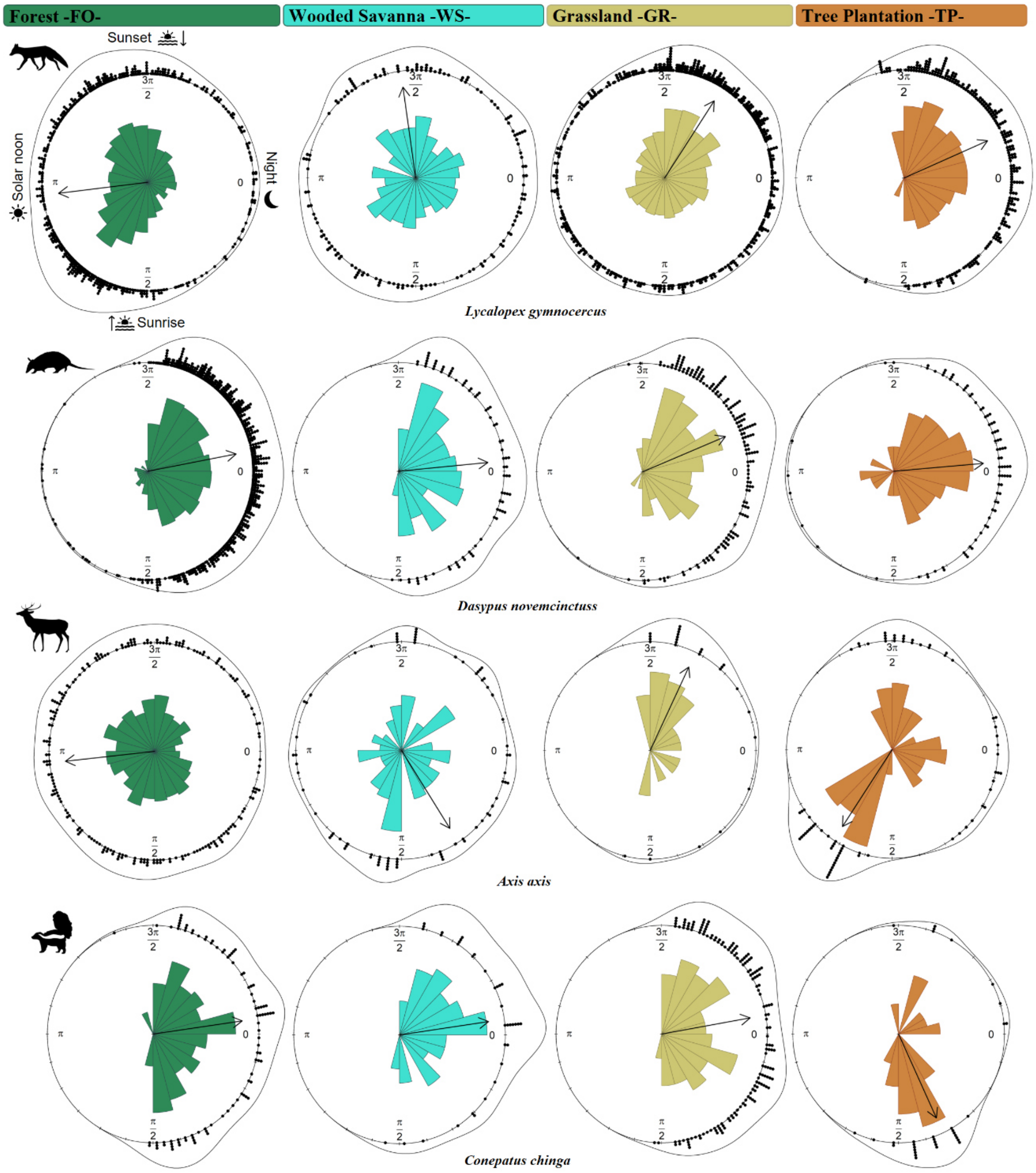

Fig. 4 Daily activity patterns for species recorded in all four habitat types (FO, WS, GR, TP). Sun-time positions are shown with clockwise rotation as follows: $3\pi/2$ = sunset, 0 = midnight, $\pi/2$ = sunrise, and π = solar noon; circle´s right-half represents nighttime and left-half represents daytime (graphical references are shown in the first circular plot of the figure). Habitat types are displayed as columns under corresponding headers and species as rows. Species are identified by silhouettes -vectorized from (De Angelo et al. 2017) and authors photographs- and names below each row. Records are represented as stacked dots, activity median as an arrow and Kernel-Density activity curve as a line outside the rose plot.

Considering the species with records in three of four habitat types, *E. sexcinctus* was the only species that showed a not uniform pattern (FO: WT=2.99, p-value<0.01, GR: WT=1.65, p-value<0.01, WS: WT=0.69, p-value<0.01) with no significant differences in the temporal budget, Act, or %Night between GR, FO**,** and WS, being nocturnal with more than 70% of the records overlapping between habitats (**Table 2**, **Fig. 3**, **Fig. 5**). *C. thous* showed no uniform activity patterns (FO: WT=0.32, p-value<0.01, GR: WT=0.84, p-value<0.01, WS: WT=0.26, p-value<0.01) with significant differences between GR and FO, and GR and WS (**Fig. 3**). While in open areas like GR a nocturnal pattern was registered, cathemeral in WS and in FO**,** but with more than 60% of activity overlap and activity peaks after sunset in all habitat types (**Table 2**, **Fig. 3**, **Fig. 5**). *H. hydrochaeris* had a not uniform pattern in FO (WT=0.47, p-value<0.01), with cathemeral activity and strong crepuscular peaks (**Fig. 3**, **Fig. 5**). In GR, the activity pattern was not uniform (WT=0.23, p-value<0.05) as well as in WS (WT=0.15, p-value<0.05), with cathemeral activity too, but with crepuscular and morning peaks in GR, and crepuscular and night peaks in WS (**Fig. 5**). Differences in Act among habitat types were significant only between FO and WS (**Table 2, Fig. 3**, **Fig. 5**).

S. scrofa showed no uniform activity patterns (FO: WT=0.41, p-value<0.01, WS: WT=0.50, p-value<0.01, TP: WT=0.44, p-value<0.01) with significant differences between all habitat type combinations (**Table 2**, **Fig. 3**, **Fig. 5**). Continuous cathemeral activity was observed in FO**,** while mostly nocturnal activity was seen on WS and TP, but with opposite peaks (before and after midnight respectively) (**Fig. 3**, **Fig. 5**).

Finally, *L. europaeus* showed no uniform activity patterns (GR: WT=5.57, p-value<0.01, WS: WT=0.24, p-value<0.01, TP: WT=0.79, p-value<0.01) with significant differences between all habitat type combinations (**Table 2**, **Fig. 3**, **Fig. 5**). Nocturnal activity was observed on GR and TP**,** and cathemeral in WS; in GR the activity level was continuous during the night, but in TP two isolated peaks were registered after sunset and during sunrise (**Fig. 3**, **Fig. 5**).

About the four species recorded in a single habitat type (**Fig. 3**, **Fig. 6**), neither of them showed uniform activity patterns along the daily sun cycle (*L. geoffroyi*: WT=0.19, p-value<0.01, *S. gouazoubira*: WT=0.28, p-value<0.01, *P. cancrivorus*: WT=1.41, p-value<0.01, *D. septemcinctus*: WT=3.47, p-value<0.01).

L. geoffroyi showed continuous cathemeral activity in FO with no strong peaks (**Fig. 3**, **Fig. 6**); same as for *S. gouazoubira* but with peaks before sunset and after sunrise. *P. cancrivorus* was nocturnal with peaks before and after midnight (**Fig. 3**, **Fig. 6**). On the contrary, *D. septemcinctus* had a diurnal activity pattern with a stable peak around solar noon (**Fig. 3**, **Fig. 6**)

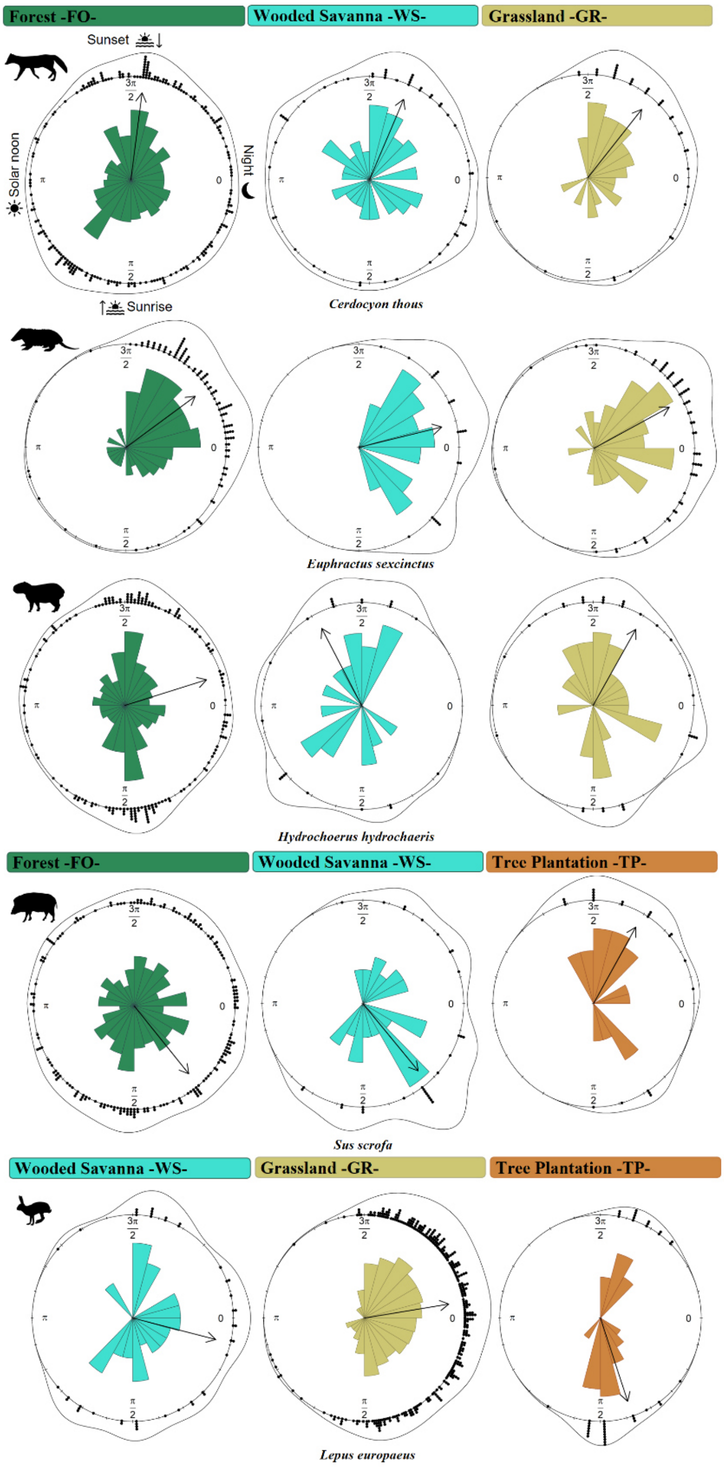

Fig. 5 Daily activity patterns for species recorded in different combinations of three habitat types (FO, WS, GR, TP). Sun-time positions are shown with clockwise rotation as follows: $3\pi/2$ = sunset, 0 = midnight, $\pi/2$ = sunrise, and π = solar noon. Habitat types are displayed as columns under corresponding headers and species as rows. Species are identified by silhouettes -vectorized from (De Angelo et al. 2017) and authors photographs- and names below each row. Records are represented as stacked dots, activity median as an arrow and Kernel-Density activity curve as a line outside the rose plot.

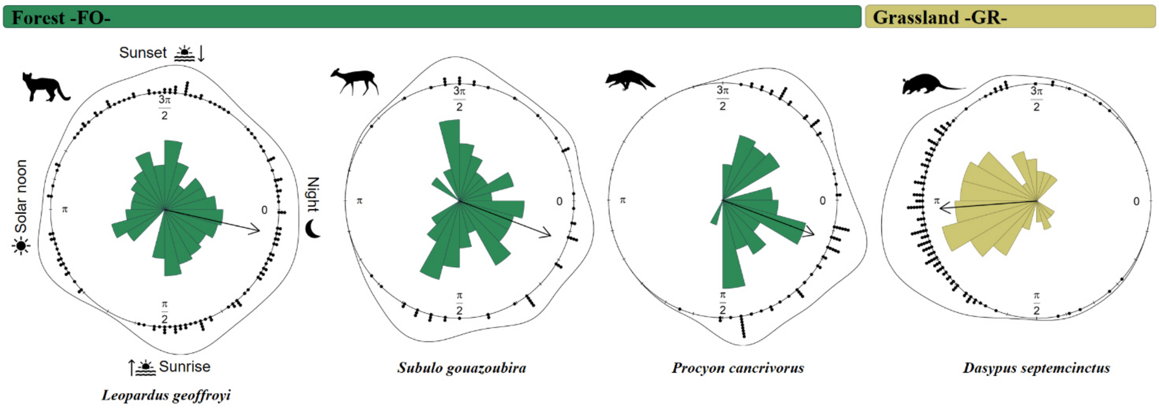

Fig. 6 Daily activity patterns for species recorded in a single habitat type (FO, WS, GR, TP). Sun-time positions are shown with clockwise rotation as follows: $3\pi/2$ = sunset, 0 = midnight, $\pi/2$ = sunrise, and π = solar noon. Habitat types are displayed as columns under corresponding headers and species as rows. Species are identified by silhouettes -vectorized from (De Angelo et al. 2017) and authors photographs- and names below each row. Records are represented as stacked dots, activity median as an arrow and Kernel-Density activity curve as a line outside the rose plot.

Species lunar activity patterns

Twelve species had sufficient nocturnal records for analyzing lunar activity patterns in different habitat types. All species showed a not uniform tendency on moonlight activity patterns in at least one habitat type. For species in more than one habitat type, except *D. novemcinctus* and *L. europaeus*, all species showed significant differences among at least one habitat pair (**Table 3**, **Fig. 7**). No lunar activity trends or habitat differences between TP (WT=0.06, p-value>0.05), WS (WT=0.04, p-value>0.05) or GR (WT=0.34, p-value<0.05) were found for *L. europaeus*, but activity was concentrated on moon illuminated stages (**Table 3**, **Fig. 7**). *D. novemcinctus* showed a uniform lunar activity pattern in FO (WT=0.08, p-value>0.05) and TP (WT=0.02, p-value>0.05), while not uniform patterns were found in GR (WT=0.17, p-value<0.05) nor in WS (WT=0.14, p-value<0.05), with a slight lunarphobic tendency (**Fig. 7**).

Table 3 Differences in species lunar activity patterns among habitat type pairs (Forest -FO-, Wooded Savanna -WS-, Grassland -GR-, Firebreak -FI-). Values shown represent: species-habitat activity overlap value (Δ) and Mardia-Watson-Wheeler p-values for circular patterns comparisons (MWW). Significant p-values (<0.05) are shown in bold and as a dash when no comparisons were performed. Species are identified by acronyms and silhouettes -vectorized from (De Angelo et al. 2017) and authors photographs-. References: Aax- *Axis axis;* Cth- *Cerdocyon thous;* Cch- *Conepatus chinga;* Dno- *Dasypus novemcinctus;* Ese- *Euphractus sexcinctus;* Hhy- *Hydrochoerus hydrochaeris,* Leu- *Lepus europaeus;* Lgy- *Lycalopex gymnocercus;* Ssc- *Sus scrofa.*

Habitat types		**Species lunar activity patterns differences**								
		Aax	***Cth***	***Cch***	***Dno***	***Ese***	***Hhy***	***Leu***	***Lgy***	***Ssc***
GR-FO	Δ	0.53	0.53	0.87	0.90	0.73	0.48	-	0.84	-
	MWW	**2e-04**	**5e-06**	0.53	0.27	**4e-04**	**1e-03**	-	**0.01**	-
GR-WS	Δ	0.65	0.69	0.77	0.86	0.74	-	0.77	0.71	-
	MWW	0.11	**0.04**	0.90	0.48	0.84	-	0.57	**6e-05**	-
GR-FI	Δ	0.58	-	0.74	0.85	-	-	0.81	0.91	-
	MWW	**0.02**	-	**0.03**	0.76	-	-	0.65	0.30	-
FO-WS	Δ	0.58	0.73	0.77	0.85	0.69	-	-	0.76	0.60
	MWW	**1e-03**	**0.01**	0.56	0.06	0.07	-	-	**0.01**	**3e-04**
FO-FI	Δ	0.76	-	0.77	0.89	-	-	-	0.86	0.74
	MWW	0.32	-	0.24	0.95	-	-	-	0.14	0.73
WS-FI	Δ	0.62	-	0.70	0.83	-	-	0.71	0.71	0.58
	MWW	0.15	-	0.22	0.35	-	-	0.65	**2e-04**	**0.01**

No trade-off between night or day activity according to moon phases was seen for *D. novemcinctus* but opposite peaks were found for *L. europaeus* in TP (Supplementary Material: Appendix IV, Fig. S5). *E. sexcinctus* showed the a lower lunarphilic tendency in FO (WT=0.11, p-value<0.05), and in open areas as WS (WT=0.33, p-value<0.05) and GR (WT=0.36, p-value<0.05) (**Table 3**, **Fig. 7**). The same occurred with *C. thous*, for FO (WT=0.69, p-value<0.05), WS (WT=0.14, p-value<0.05) and GR (WT=0.29, p-value<0.05) but with significant differences among all habitat pairs (**Table 3**, **Fig. 7**).

Lunarphilic tendencies were seen in FO for *S. scrofa* (WT=0.28, p-value<0.05) and *A. axis* (WT=0.27, p-value<0.05) as well, but also in TP (WT=0.09 and WT=0.08 respectively with p-value<0.05) with activity during all moon illuminated phases; same as for the previous species, in WS (WT=0.29 and WT=0.22 respectively with p-value<0.05) the activity was lunarphobic, as in GR (WT=0.32, p-value<0.05) for *A. axis* too (**Table 3**, **Fig. 7**). For the opposite, *L. gymnocercus* had lunarphilic tendencies on WS (WT=0.47, p-value<0.05), same as in FO (WT=0.28, p-value<0.05), but no tendency was seen in TP (WT=0.08, p-value>0.05) or GR (WT=0.06, p-value>0.05) (**Table 3**, **Fig. 7**). *C chinga* had non-significant activity peaks on full moon in WS (WT=0.18, p-value<0.05), lunarphobic tendencies in TP (WT=0.12, p-value<0.05) and no tendencies on FO (WT=0.10, p-value<0.05) or GR (WT=0.11, p-value<0.05) (**Table 3**, **Fig. 7**).

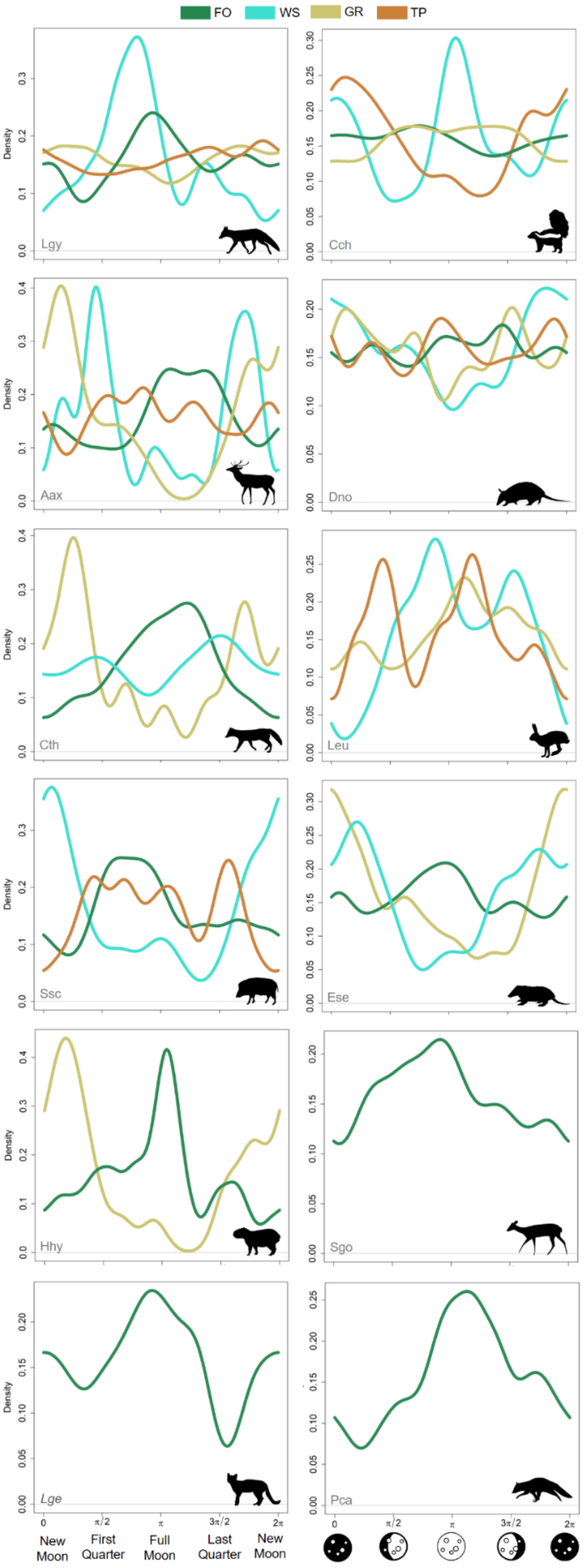

Fig. 7 Moon activity patterns for species recorded different habitat type (FO, WS, GR, TP). Moon-phases are shown in the X-axis as followed: 0 = New Moon, $\boldsymbol{\pi/2}$ = First Quarter, $\boldsymbol{\pi}$ = Full Moon, and $\boldsymbol{3\pi/2}$ = Last Quarter; Habitat types are displayed with distinct colors. Species are identified by silhouettes -vectorized from (De Angelo et al. 2017) and authors photographs- and acronyms. Note the different values on Y-axis. References: Aax- *Axis axis*; Cth- *Cerdocyon thous*; Cch- *Conepatus chinga*; Dno- *Dasypus novemcinctus*; Ese- *Euphractus sexcinctus*; Hhy- *Hydrochoerus hydrochaeris*; Leu- *Lepus europaeus*; Lge- *Leopardus geoffroyi*; Lgy- *Lycalopex gymnocercus*; Pca- *Procyon cancrivorus*; Sgo- *Subulo gouazoubira*; Ssc- *Sus scrofa*.

H. hydrochaeris showed clear lunarphilic tendency in FO (WT=0.48, p-value<0.05), the habitat with more dense tree canopy cover, while a significant lunarphobic tendency was found in open areas of GR (WT=0.33, p-value<0.05) with activity peaks around new moon (**Table 3**, **Fig. 7**). The same lunarphilic tendency in FO was registered in *S. gouazoubira* (WT=0.14, p-value<0.05), *L. geoffroyi* (WT=0.23, p-value<0.05) and *P. cancrivorus* (WT=0.25, p-value<0.05).

Within FO, a shift between nocturnal and diurnal activity was seen for these last three species and for *C. thous, L. gymnocercus, A. axis* and *S. scrofa*, according to the moon phase: an increase in nocturnal activity and a decrease in daytime activity during the full moon (Supplementary Material: Appendix IV, Fig. S5). The same occurred in WS and TP for *A. axis* and in TP for *L. gymnocercus,* while the opposite trend was seen for this species and *C. thous* in WS (Supplementary Material: Appendix IV, Fig. S5).

Discussion

Species patterns of habitat use intensity have been clearly more studied when considering afforestation effects (e.g. Cravino and Brazeiro 2021; Iezzi *et al.* 2020; Martínez-Lanfranco *et al.* 2022). This study represents the first one in *Eucalyptus* plantations from grassland afforestation, considering temporal pattern changes. In Uruguay, it also represents the first study on mammals' activity patterns considering solar and lunar stages. Since activity levels and patterns recorded by camera traps correspond to several individuals from each species, they reflect population-level measures that could easily be compared between different locations or times.

No significant differences were found in temporal behaviors across seasons as in some other regions (Botts, Eppert, Wiegman, Rodriguez, *et al.* 2020; Michalski and Norris 2011), although in most studies, animal activity patterns were affected by seasonal changes (e.g. Donati and Borgognini-Tarli 2006; Haughey 1973; Ikeda *et al.* 2016; Botts, Eppert, Wiegman, Blankenship, *et al.* 2020). But slight temporal shifts were found for *H. hydrochaeris* (peaks around sunrise in the warm season, and around sunset in the cold season), *A. axis* (opposite to *H. hydrochaeris*), and *L. geoffroyi* (temporal peak in daytime in the cold season). In these Uruguayan areas, seasonal variation might be compensated by using the sun-clock instead of the clock-time considering the latitudinal variation of day and night length, thermal constraints, and luminosity according to the moon and cloud cover (Daan and Aschoff 1975; Nouvellet *et al.* 2012; Bennie *et al.* 2014).

Changes in landscape patterns may provoke changes in ecosystems composition as well as in biodiversity, spatial and temporal patterns, and behaviors (Liu and Andersson 2004; Norris *et al.* 2010; Wong and Candolin 2015; Iglesias-Carrasco *et al.* 2022; Liu *et al.* 2022). But in this research, mammals did not show any evidence of adjustment in their temporal behavior as plantations cover increased in the landscape, even in the large gradient assessed (<10 to >80% plantation cover). However, based on descriptive and quantitative analyses, this study was able to describe how species activity changed daily and among lunar phases, finding significant differences at the local scale between native (FO, WS, and GR) and afforested (TP) habitats despite their close spatial proximity within each landscape.

Species solar activity patterns

Generally, in human-modified areas diurnal activity has been identified as a barrier to movement between favorable patches (Daily and Ehrlich 1996; Donati and Borgognini-Tarli 2006; Wong and Candolin 2015), while cathemeral activity increases with habitat fragmentation (Norris *et al.* 2010; Bennie *et al.* 2014) as well as nocturnality as it reduces threats (Bennie *et al.* 2014; Gaynor *et al.* 2019; Muñoz-García *et al.* 2018), as seen in oil palm plantations (Pardo *et al.* 2021) and in abandoned plantations (Rodríguez-Gómez and Fontúrbel 2020). While no differences were found among landscapes along the afforestation gradient studied, the three conditions were observed: cathemeral and nocturnal activity were the patterns seen for 12 of the 13 species considered. Diurnality was very rare in these landscapes, the only species with fully diurnal pattern, *D. septemcinctus,* was found almost exclusively in the grassland dominated landscape (TPC≤10%). This could be interpreted as an homogenization of temporal wildlife behavior

(Iglesias-Carrasco *et al.* 2022), losing diurnal species. Due to habitat loss in tree-planted landscapes, this armadillo is probably the most affected Uruguayan mammal by grassland afforestation (Brazeiro *et al.* 2018; Cravino and Brazeiro 2021).

TP showed continuous temporal use only by *L. gymnocercus* and *D. novemcinctus*. In previous Uruguayan studies, generalist species were the most common and frequent on tree plantations, especially the two mentioned (Brazeiro *et al.* 2018; Cravino and Brazeiro 2021). Given that generalist species are usually the more adapted to new afforested transformed environments having higher behavioral plasticity (da Silva 2001; da Silveira 2005; Lyra-Jorge *et al.* 2008; Andrade-Núñez and Aide 2010; O'Callaghan *et al.* 2016; Dotta and Verdade 2011; Mosquera-Guerra *et al.* 2018; Iezzi *et al.* 2020, 2021; Cravino and Brazeiro 2021; Iglesias-Carrasco *et al.* 2022), our results were expected. In Uruguay, it has been recorded a high number of burrows of *D. novemcinctus* in *Eucalyptus* plantations, especially towards the edges and in FI (Cravino and Brazeiro 2021), and in this study showed continuous temporal use of TP, no different than in native habitats. This behavior pattern reinforces the idea that this species is adapted to *Eucalyptus* plantations. The other species with records in TP (*A. axis, C. chinga, S. scrofa,* and *L. europaeus*) showed non-continuous patterns but isolated peaks. In human-modified habitats it was shown that species are forced into shorter activity time-windows (Shamoon *et al.* 2018; Iglesias-Carrasco *et al.* 2022; Pardo *et al.* 2021). This could also be reflecting the use of FI, TP component with a higher number of records, as corridors or connectors to more suitable native habitats with more continuous use by these species (Cravino and Brazeiro 2021). Various studies have already demonstrated that mammals tend to use open environments, such as trails, FI, or roads, to circulate more efficiently through the landscapes (James and Stuart-Smith 2000; Lantschner 2012). In temperate South America, there are some antecedents of this spatial use of FI by mammals in afforested landscapes, like in Argentina (Lantschner 2012; Decarre 2015), Brazil (da Silva 2001; da Silveira 2005; Timo *et al.* 2015), Chile (McFadden and Dirzo 2018) and Uruguay (Cravino and Brazeiro 2021).

For two species it was observed a consistent pattern of preference to open native habitats (GR, WS) in the darkness (during the night), and covered habitats (FO, TP) during daylight. These patterns were seen in several previous works (Preisler *et al.* 2006; Godvik *et al.* 2009; Gaynor *et al.* 2019, 2021; Botts, Eppert, Wiegman, Rodriguez, *et al.* 2020; Richter *et al.* 2020). This clear temporal tendency of visiting open areas mostly during the night and visiting covered forest areas during the day was seen for *A. axis*, and *L. gymnocercus*. For other species, the nocturnal pattern in open habitats was observed, but cathemeral activity was registered in FO, as for *S. scrofa* and *C. thous*, or with no records in FO as with *L. europaeus.*

Species lunar activity patterns

Previously, it was stated that nocturnality reduces threats (Bennie *et al.* 2014; Gaynor *et al.* 2019), but does it always? About lunar phases' tendencies, all nine species with records in FO (*L. gymnocercus, A. axis, C. thous, S. scrofa, E. sexcinctus, H. hydrochaeris, L. geoffroyi, S. gouazoubira,* and *P. cancrivorus*), had a lunarphilic trend in this cover habitat type, with temporal activity concentrated on full moon. The same happened with TP for the species with enough records to show a tendency (*A. axis* and *S. scrofa*). The opposite lunarphobic trend was registered in open habitats: in GR for 5 of 6 species with a lunar trend (*A. axis, D. novemcinctus, C. thous, E. sexcinctus,* and *H. hydrochaeris*) and in WS for five from 8 species with a trend (*A. axis, D. novemcinctus, C. thous, S. scrofa* and *E. sexcinctus*). Like in this work, "lunar phobia" has been also previously documented in several species by reducing the use of open areas or areas were moonlight easily passes through (Morrison 1978; Gilbert and Boutin 1991; Kotler *et al.* 1991; Saldaña-Vázquez and Munguía-Rosas 2013; Prugh and Golden 2014) and for the opposite, "lunar philia" in cover areas (Karlsson *et al.* 2002; Gursky 2003; Michalski and Norris 2011; Saldaña-Vázquez and Munguía-Rosas 2013), but not all species since other factors could be operating too (Pratas-Santiago *et al.* 2016, 2017; Botts, Eppert, Wiegman, Blankenship, *et al.* 2020). Here, *L. europaeus* was the exception that showed activity in all moon stages except new moon in all habitat types with different peaks, and *L. gymnocercus* and *C. chinga* were the only ones with lunarphilic tendencies in WS. This last species was the only one with lunarphobic trends in TP, probably related to the avoidance of predation risk, driver explained in the next section.

Temporal niche drivers

Since species are connected to each other within an ecological network, behavioral responses can affect species interactions, including foraging, predation, and competition. Three main interconnected drivers have been used to explain species solar and lunar patterns. The first one, may be the offset between predation/hunting pressure and feeding time (Iglesias-Carrasco *et al.* 2022). Herbivores and other prey species must balance the need to obtain foraging resources against avoiding predation (Prugh and Golden 2014; Moll *et al.* 2017; Fattebert *et al.* 2019), and this forage-safety trade-off could change through space and time (Lone *et al.* 2017; Botts, Eppert, Wiegman, Rodriguez, *et al.* 2020; Botts, Eppert, Wiegman, Blankenship, *et al.* 2020; Frey *et al.* 2017). While open habitats such as GR or WS may provide high-quality forage (Hebblewhite *et al.* 2008; Godvik *et al.* 2009), covered habitats such as FO and TP may represent protection from predators (Fardell *et al.* 2021). But not only wild preys avoid predation; for carnivores and other hunting target animals, humans are perceived as a predation risk to be considered too (Stafford *et al.* 2017; Mendes *et al.* 2019; Gaynor *et al.* 2019, 2021; Carreira *et al.* 2020; Richter *et al.* 2020; Iglesias-Carrasco *et al.* 2022). This "landscape of fear" is dynamic rather than constant (Dammhahn *et al.* 2022; Palmer *et al.* 2022), and is items to be pushing some species to become increasingly nocturnal (Bennie *et al.* 2014; Gaynor *et al.* 2019; Iglesias-Carrasco *et al.* 2022), to be more frequent in cover areas to reduce encounters with humans (Little *et al.* 2016; Gaynor *et al.* 2018; Richter *et al.* 2020) or in open areas during new moon (Morrison 1978; Gilbert and Boutin 1991; Kotler *et al.* 1991; Saldaña-Vázquez and Munguía-Rosas 2013), or even avoid places and times where they are more likely to be pursued (Carter *et al.* 2012; Tucker *et al.* 2018; Pardo *et al.* 2021; Iglesias-Carrasco *et al.* 2022). The exotic species *L. europaeus*, *A. axis,* and *S. scrofa* are legally or illegally hunted (depending on the species) in Uruguay, as well as several native species, such as *H. hydrochaeris* and the armadillos (Chouhy and Dabezies 2021). Foxes (such as *L. gymnocercus*) and wild cats (such as *L. geoffroyi*) are being also illegally hunted by conflicts with sheep production and poultry (González *et al.* 2016; Zambra *et al.* 2022). In this context, FO could be offering these species spatial protection, but also TP when using the FI as a corridor surrounded by tree cover (Cravino and Brazeiro 2021), in contrast to GR and WS.

Regarding moonlight, some sea predators dive deeper into the ocean to increase their foraging success during full moon (Horning and Trillmich 1997) and some terrestrial predators take advantage of their "night vision" (Schwab *et al.* 2002; Ollivier *et al.* 2004) while some mammal preys, insects and amphibians reduce their activity to avoid predation (Tuttle *et al.* 1982; Lang *et al.* 2006; Prugh and Golden 2014; Soulsbury 2021). Therefore, daylight and moonlight avoidance might be a strategy used by some species to reduce the risk of predation (Prugh and Golden 2014).

Considering this, the second possible driver, deeply connected to predation risk, is related to the species reaction to the luminosity (Fernandez-Duque and Erkert 2006; Fernández-Duque *et al.* 2010; Gerkema *et al.* 2013; Prugh and Golden 2014; Pratas-Santiago *et al.* 2017; Wu *et al.* 2017; Botts, Eppert, Wiegman, Blankenship, *et al.* 2020; Gaynor *et al.* 2021). Most species prefer, and several works found that both cloud cover (which modifies moonlight) and tapetum lucidum type of the species as a proxy of night vision acuity (Schwab *et al.* 2002; Ollivier *et al.* 2004), have a significant influence over some mammals that are active at night during the lunar cycle, but also have a significant effect on whether animals are active during the night versus day (Prugh and Golden 2014; Pratas-Santiago *et al.* 2017; Botts, Eppert, Wiegman, Blankenship, *et al.* 2020). In this work, temporal variation of night and day records according to lunar phases was also detected for most species among several habitat types.

Some mammals have no tapetum: most rodents (as *H. hydrochaeris*), lagomorphs (as *L. europaeus*), and xenarthrans (as armadillos: *D. novemcinctus, D. septemcinctus* and *E. sexcinctus*). Species with no tapetum do not rely on visual senses and have poor night vision so they used to be diurnal (Ollivier *et al.* 2004), like D. *septemcinctus* in this work, or when nocturnal they are less active during the full moon or directly unaffected (Ollivier *et al.* 2004; Prugh and Golden 2014), like *D. novemcinctus*, *L. europaeus*, *E. sexcinctus* in all habitats. Similarly, armadillos had no lunar pattern in Huck *et al.* (2017) and in Botts *et al.* (2020) and were slightly lunarphobic in Pratas-Santiago *et al.* (2017). When present, all tapetum variants increase retinal sensitivity by reflecting light (Ollivier *et al.* 2004). Carnivores, that have choroidal tapetum cellulosum and therefore greater light reflectance (Schwab *et al.* 2002; Ollivier *et al.* 2004), would be more active in full moon (Prugh and Golden 2014), as seen in this work. Ungulates, as deer species (*A. axis* and *S. gouazoubira*), that have choroidal tapetum fibrosum and good night vision (Ollivier *et al.* 2004; Schwab *et al.* 2002), might be less active in the full moon (Prugh and Golden 2014), as seen for *A. axis* in this work but opposite for *S. gouazoubira* as in Huck *et al.* (2017) but not in Botts *et al.* (2020). With these two deer species, temporal shift for avoiding competition could be happening (Cravino *et al.* 2021).

The third driver is related to niche partitioning as a mechanism used by sympatric mammal species to mitigate competition and achieve coexistence (Schoener 1974; Di Bitetti *et al.* 2009; Davis *et al.* 2018), even between small mammals (Soulsbury 2021). Therefore, species ecologically similar or equivalent, should reduce the overlap in the use of resources along time, space, and/or diet (Schoener 1974). Considering the spatial niche, some of them tend to spatially co-occur rather than avoid, like the foxes *L. gymnocercus* and *C. thous* in this work, probably due to having similar habitat and food requirements (Vieira and Port 2007; Di Bitetti *et al.* 2009, 2022; Davis *et al.* 2018; Bossi *et al.* 2019). Temporally, *L. gymnocercus* generally shows a cathemeral activity pattern, while *C. thous* were mostly nocturnal, as seen in other regions in which these species cooccur (Vieira and Port 2007; Di Bitetti *et al.* 2009, 2022; Faria-Corrêa *et al.* 2009; Nanni 2015). Considering moon phases, temporal segregation was also detected in wooded savannahs -WS-, where *L. gymnocercus* was lunarphillic, while *C. thous* was lunarfobic. Spatio-temporal segregation could be also seen among the armadillos (*D. septemcicntus* and *D. novemcinctus*) and deer (*A. axis* and *S. gouazoubira*).

Methodological considerations

The decision of working with sun-time instead of clock-time in Southern latitudes was accurate, since day length changed notably along the year, with shorter days in the cold season (shorter day length: 9.74 hours, earlier sunrise: 07:21am, later sunset: 5:42PM) and longer ones in the warm season (shorter day length: 14.26 hours, earlier sunrise: 05:01AM, later sunset: 08:45PM). Therefore sun-time reflected more clearly the activity patterns chosen by the species along habitat types.

Besides the results found, solar and lunar tendencies showed the importance of survey design, considering not only the spatial distribution of sampling stations, also the temporal length of the studies. Species responses could not be detected if not all habitat types were considered, nor if sampling stations remained active for less than a moon cycle (27 days).

Concluding remarks

This represents the first study of temporal patterns in grassland afforestation with *Eucalyptus* plantations. The local habitat type determined the species activity patterns, independently from *Eucalyptus* plantation cover at the landscape level. Habitat type affected most species temporal niche, finding significant differences between native (FO, WS, and GR) and afforested (TP) habitats despite their close spatial proximity within each landscape. We found that most species adjust their daily activity pattern at *Eucalyptus* plantation, basically reducing their temporal activity to narrower temporal intervals, suggesting the use of FI as corridors or connectors to native habitats. Only a few generalist species showed the same activity rhythms both at their native habitats and TP.

Using sun-time for temporal analysis allowed this work to perceive how species make their temporal and spatial decisions based on sunlight and moonlight conditions. Sun-time and lunar activity patterns variation among habitat types could be explained as possible reactions to predation risk, hunting pressure, foraging, and competition according to habitat cover availability and to the sun and the moon luminosity.

Given the projected expansion of afforestation in Uruguay (Brazeiro *et al.* 2020), focusing research efforts on understanding species spatiotemporal responses and how they cope in these anthropized landscapes is vital for conservation and decision making.

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Conflict of interest disclosure

The authors have no relevant financial or non-financial interests to disclose.

Data availability statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Supplementary material for

Tick, tock… says the moon and the sun: mammals' activity patterns in landscapes with *Eucalyptus* plantation

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This file includes Appendix I-IV, Table S1-S4, and Fig. S1-S5.

Appendix I – Study Area and Methods Details

Study area

Within all considered landscapes, native habitats and tree plantations were surveyed. Within the tree plantations, two components were surveyed and considered as differential habitat types (Cravino and Brazeiro 2021): mature tree stands -TS- and firebreaks -FB- (**Fig S1**). Three native habitat types were considered: close canopy forests (referred to as forests -FO- hereafter), open canopy forests (referred to as wooded savanna -WS- hereafter), and grasslands -GR- (**Fig S1**).

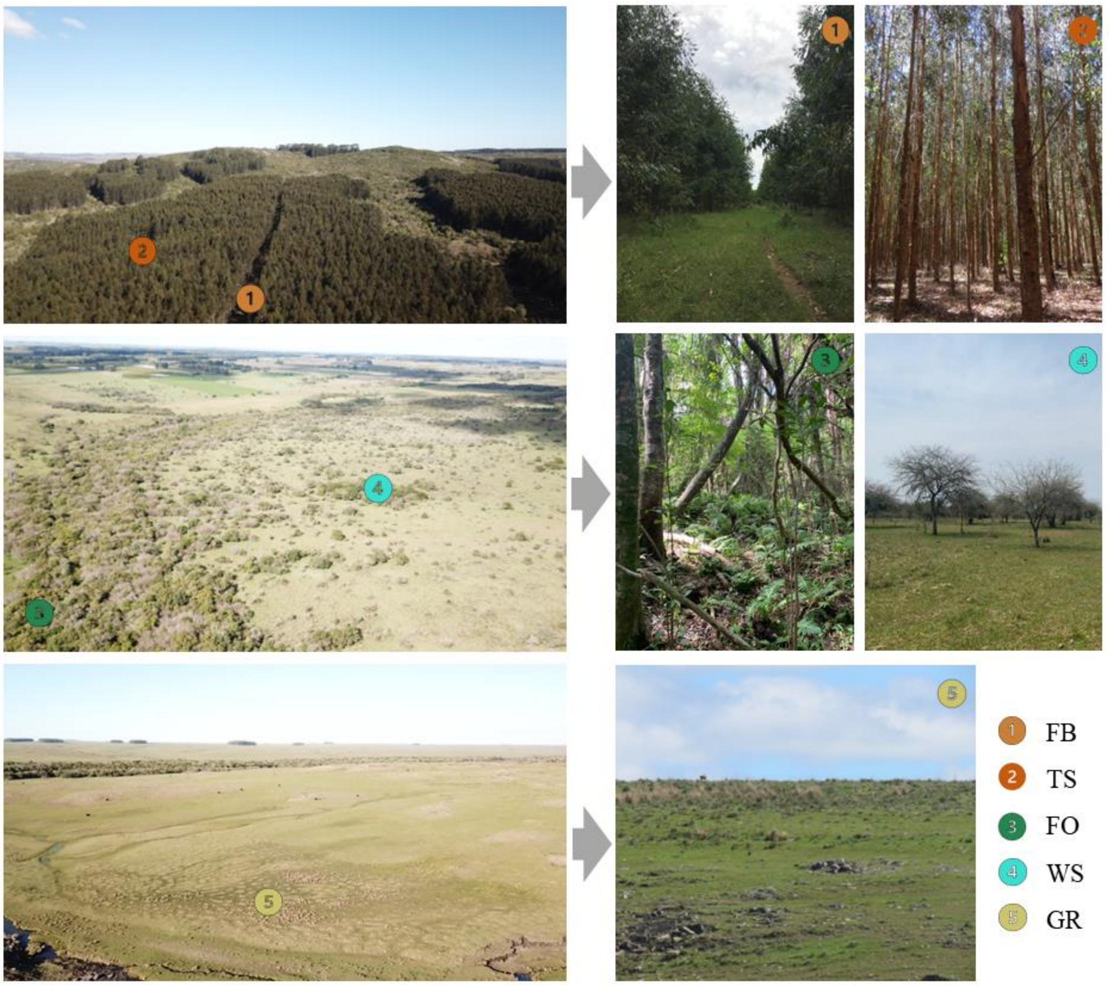

Fig. S1 Illustrative photographs of habitat types surveyed.

Camera trap survey

The camera traps were active 24 hours a day throughout the sampling period and were programmed to take three 10-megapixel images upon activation by movement and temperature differences, with a high sensitivity mode and a subsequent 15-second latency. The camera model features a trigger speed of 0.5 seconds (**Fig S2**). Cameras were installed in trees or poles facing South or North to avoid false triggers due to direct sunlight exposure. Baits were not used, and adjacent vegetation that could activate or cover the cameras was removed to optimize detection and facilitate species recognition. The placement height was between 50 and 70cm, according to the average height of potential species, in order to reduce variations in detectability by body size and /or camera capture angle (Meek *et al.* 2016). The optimal detection distance was estimated at 3 meters from the placement site.

Fig. S2 Camera trap deployment.

Solar and lunar data preparation

Variables shown in **Table S1** are the ones considered for the species activity patterns classification. Solar positions, lunar phases and lunar positions according to local time and space were obtained with the suncalc R package (Thieurmel and Elmarhraoui 2019).

Table S1 Solar and lunar variables.

Sun Position	Abbreviation	Definition	Characteristics/Usage
Sunrise Start	SRS	Time in which the top edge of the sun appears on the horizon.	It represents $\frac{\pi}{2}$ in activity patterns plots.
Sunrise End -Dawn-	SRE	Time after the bottom edge of the sun touches the horizon.	It represents the period in the day when light from the sun begins to appear in the sky. So, this time is considered, in this research, as the start of the **day** period.
Sunset Start	SSS	Time in which the bottom edge of the sun touches the horizon.	It represents $\frac{3\pi}{2}$ in activity patterns plots.
Sunset End -Dusk-	SSE	Time in which the sun disappears below the horizon.	It represents the time before night when the day is losing its light, but it is not yet completely dark. So, this time is considered, in this research, as the start of the **night** period.
Twilight (Crepuscular)	-	The time between day and night when there is light outside, but the sun is below the horizon. The morning twilight is often called Dawn (SRE), while the evening twilight is also known as Dusk (SSE).	For a practical definition, it is considered a word reference of species activity around **sunset** (time between SSS and SSE) and **sunrise** (time between SRS and SRE).
Moonrise	MRI	Time in which the top edge of the moon appears on the horizon.	Considered the starting time of the night period with moon influence.
Moonset	MSE	Time in which the moon disappears below the horizon.	Considered the end time of the night period with moon influence.
Moon altitude	MA	Moon altitude considering the horizon.	Positive altitudes were considered important for moon influence analysis.

Appendix II – Species recorded

The regional pool of medium-large mammals in the study areas is restricted to 13 species with at least 20 records from 6 Orders and 14 Families. The full list of species and their records is shown in the **Table S2**.

Table S2 Species records according to landscape tree plantation cover -TPC- class (≤10, ≤25, ≤40, ≤65, ≤80, ≤100%) and habitat type (Forest -FO-, Wooded savanna -WS-, grassland -GR-, firebreak -FI- and tree stand -TS-).

Order	**Family**	**Scientific name**	**Common name**	**Ref. code**	**Landscapes**						**Habitat types**				
					≤10	**≤25**	**≤40**	**≤65**	**≤80**	**≤100**	**FO**	**WS**	**GR**	**FI**	**TS**
Artiodactyla	Cervidae	*Axis axis*	Axis Deer	**Aax**	49	115	1	149	-	88	209	76	26	75	16
Artiodactyla	Cervidae	*Subulo gouazoubira*	Gray Brocket Deer	**Sgo**	-	-	12	-	38	-	50	-	-	-	-
Artiodactyla	Suidae	*Sus scrofa*	Wild Boar	**Ssc**	4	54	61	49	44	49	190	30	15	22	4
Carnivora	Canidae	*Cerdocyon thous*	Crab-eating Fox	**Cth**	33	24	156	71	22	16	219	51	36	16	-
Carnivora	Canidae	*Lycalopex gymnocercus*	Pampas fox	**Lgy**	331	100	129	469	213	308	558	147	595	253	17
Carnivora	Felidae	*Leopardus geoffroyi*	Geoffroy's Cat	**Lge**	7	2	81	42	27	10	138	10	12	9	-
Carnivora	Mephitidae	*Conepatus chinga*	Molina's Hog-nosed Skunk	**Cch**	79	3	21	87	29	101	92	35	159	33	1
Carnivora	Procyonidae	*Procyon cancrivorus*	Crab-eating Raccoon	**Pca**	7	11	51	13	8	1	69	5	10	7	-
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded Armadillo	**Dno**	37	40	481	263	201	115	793	79	168	78	19
Cingulata	Dasypodidae	*Dasypus septemcinctus*	Seven-banded Armadillo	**Dse**	-	-	1	6	-	118	-	-	125	-	-
Cingulata	Euphractidae	*Euphractus sexcinctus*	Yellow Armadillo	**Ese**	-	4	58	80	32	26	109	21	63	7	-
Lagomorpha	Leporidae	*Lepus europaeus*	European Hare	**Leu**	84	3	29	2	2	319	10	43	331	43	12
Rodentia	Cavidae	*Hydrochoerus hydrochaeris*	Capybara	**Hhy**	1	55	16	32	2	125	177	22	32	-	-

Appendix III – Cofounding factors

Eight study areas were grouped into six landscape types according to the percentage of tree plantation cover -TPC- within a 5km buffer: up to 10% (TPC ≤ 10%), up to 25% (10% < TPC ≥ 25%), up to 40% (25% < TPC ≥ 40%), up to 65% (40% < TPC ≥ 65%), up to 80% (65% < TPC ≥ 80%) and up to 100% (80% < TPC ≥ 100%). Within each landscape class, five habitat types were surveyed when present: Firebreak -FI-, Tree Plantation Stand -TS-, Forest -FO-, Wooded Savanna -WS- and Grassland -GS-.

The number of records was not enough in TP. Significance tests were performed to compare species solar and lunar activity patterns between seasons (Warm, Cold), landscapes (≤10, ≤25, ≤40, ≤65, ≤80 and ≤100%) and habitat types (TP, FO, WS, GS). There were no significant differences among species activity level -Act- or night records -%Night- considering seasons or landscapes (**Table S3**, **Fig. S3**, **Fig. S4**). Besides having no differences in Act and Night between species, three showed a shift in activity peaks: *Leopardus geoffroyi* had a diurnal peak in the cold season, while crepuscular-nocturnal in the warm season; *Axis axis* during sunrise in the cold season and during sunset in the warm season, and the opposite was seen for *Hydrochoerus hydrochaeris* (**Fig. S3**).

Table S3 Significance values for species activity level (Act) and percentage of night records (%Night) considering the season, landscape, and habitat type. Significant p-values (<0.05) are shown in bold.

Species (≥ 20 records)		**Significance differences *p-values***					
		Season		**Landscape**		**Habitat**	
Acronym	**Scientific name**	**Act**	**%Night**	**Act**	**%Night**	**Act**	**%Night**
Aax	*Axis axis*	0.8321	0.8734	0.1013	0.1084	**0.0131**	**0.0306**
Cth	*Cerdocyon thous*	0.5637	0.3495	0.2231	0.6834	**0.0431**	**0.0449**
Cch	*Conepatus chinga*	0.8765	0.4589	0.3567	0.4984	**0.0403**	**0.0498**
Dno	*Dasypus novemcinctus*	0.9482	0.9823	0.9495	0.4983	0.0534	0.2983
Dse	*Dasypus septemcinctus*	0.8932	0.8375	-	-	-	-
Ese	*Euphractus sexcinctus*	0.7984	0.6983	0.8976	0.4976	0.1092	0.1985
Hhy	*Hydrochoerus hydrochaeris*	0.8934	0.5069	0.5786	0.6983	**0.0456**	**0.0298**
Lgeo	*Leopardus geoffroyi*	0.6859	0.3094	0.7685	0.4827	-	-
Leu	*Lepus europaeus*	0.8976	0.5298	0.6754	0.9863	**0.0491**	**0.0492**
Lgy	*Lycalopex gymnocercus*	0.4809	0.4592	0.7569	0.2842	0.1673	**0.0309**
Sgo	*Subulo gouazoubira*	0.8965	0.5492	-	-	-	-
Pca	*Procyon cancrivorus*	0.7823	0.2984	-	-	-	-
Ssc	*Sus scrofa*	0.7384	0.4587	0.6721	0.9843	**0.0479**	**0.0500**

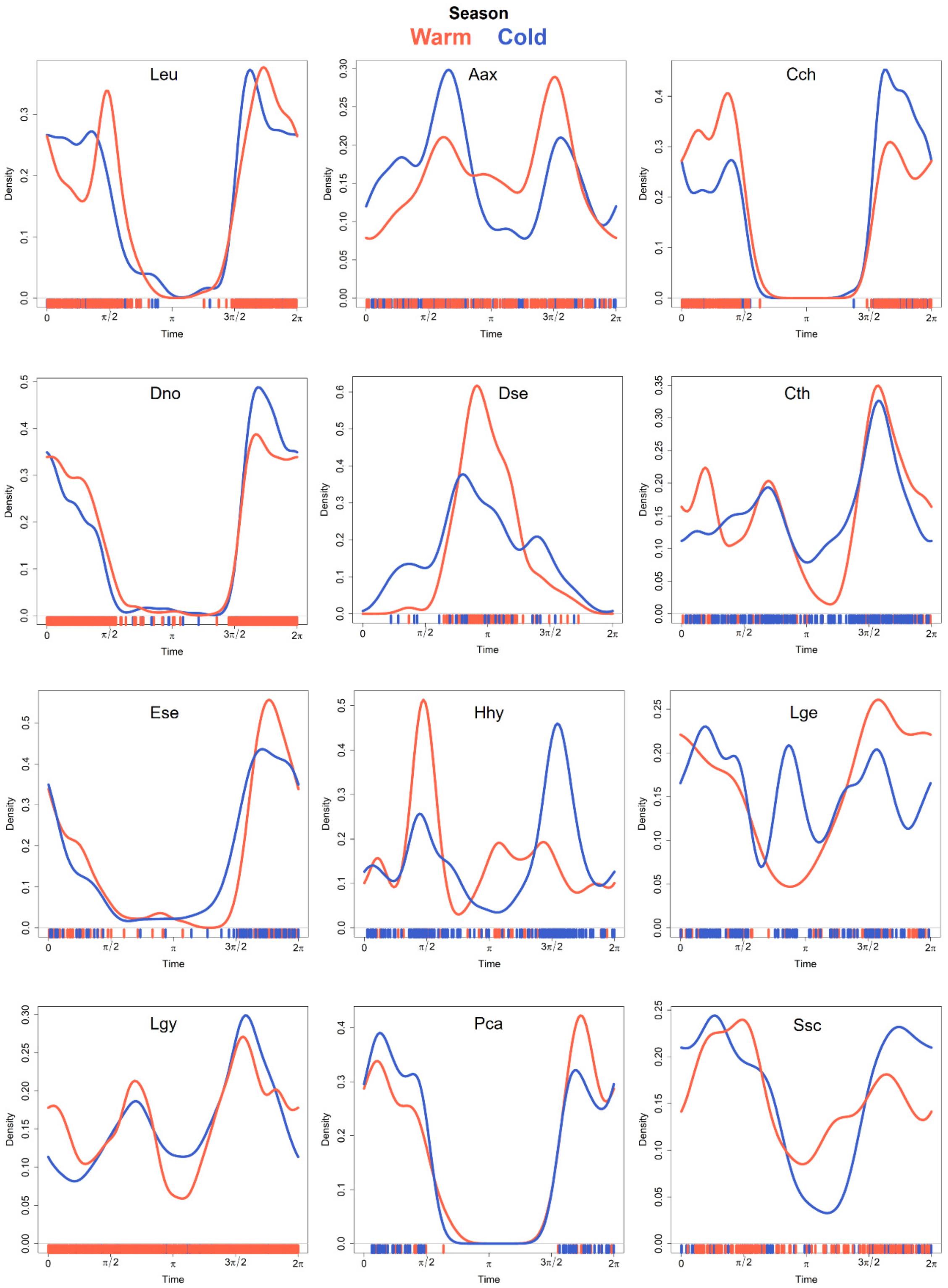

Fig. S3 Density curve of activity patterns for species according to seasons (Cold and Warm). Sun-time positions are as follows: 3π/2 = sunset, 0 = midnight, π/2 = sunrise, and π = solar noon; circle´s right-half represents nighttime and left-half represents daytime (graphical references are shown in the first circular plot of the figure). Habitat types are displayed as columns under corresponding headers and species as rows. Species are identified by acronyms. References: Aax- *Axis axis*; Cth- *Cerdocyon thous*; Cch- *Conepatus chinga*; Dno- *Dasypus novemcinctus*; Dse- *Dasypus septemcinctus*; Ese- *Euphractus sexcinctus*; Hhy- *Hydrochoerus hydrochaeris*, Leu- *Lepus europaeus*; Lge- *Leopardus geoffroyi*; Lgy- *Lycalopex gymnocercus*; Pca- *Procyon cancrivorus*; Ssc- *Sus scrofa*. Note the different values on Y-axis.

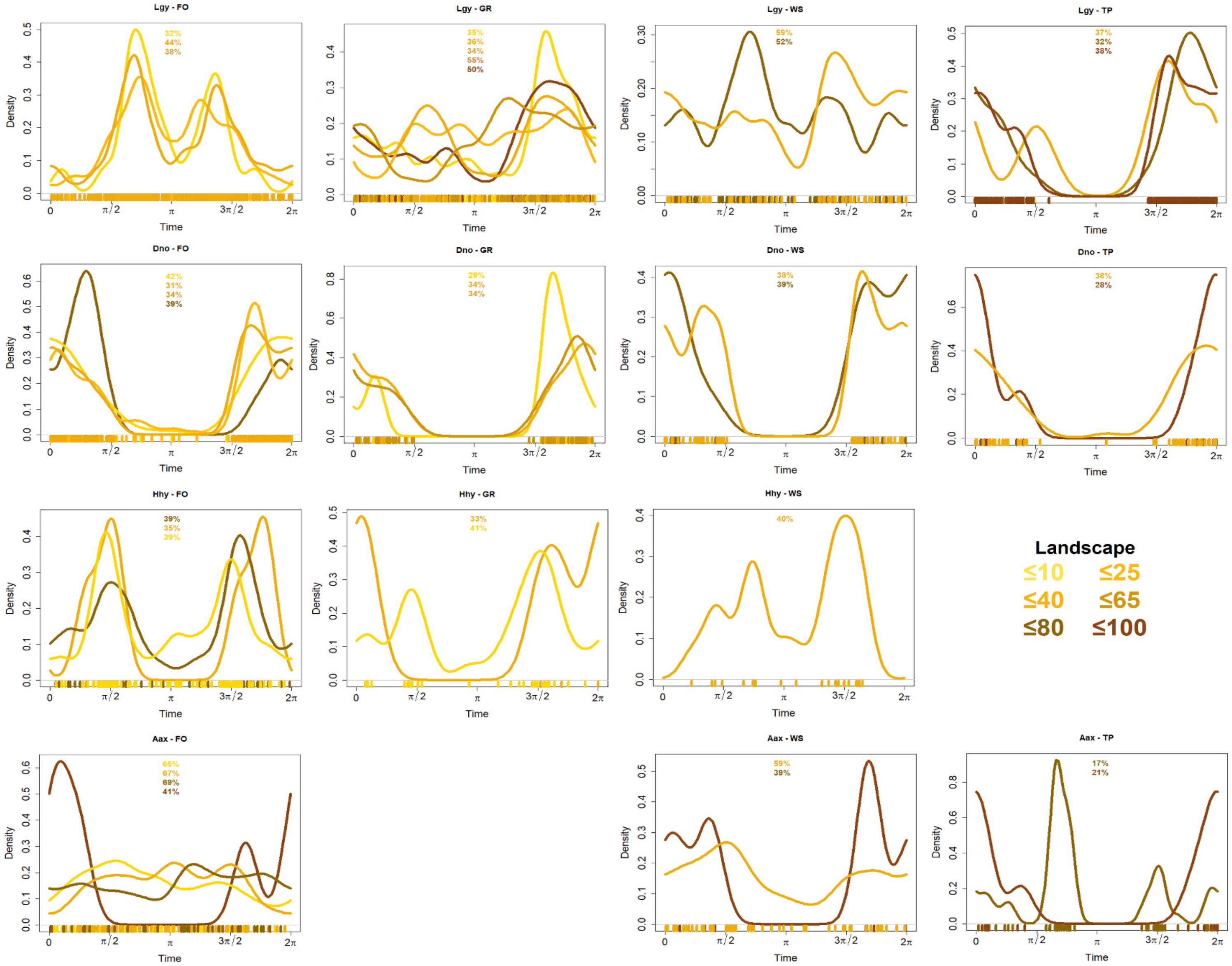

Fig. S4 Density curve of activity patterns for species according to landscapes (≤10, ≤25, ≤40, ≤65, ≤80, and ≤100% TPC) and habitat types (Forest -FO-, Wooded Savanna -WS-, Grassland -GR-, Tree Plantation -TP-). Sun-time positions are as follows: 3π/2 = sunset, 0 = midnight, π/2 = sunrise, and π = solar noon. Habitat types are displayed as columns and species as rows. Species are identified by acronyms. References: Aax- *Axis axis*; Dno- *Dasypus novemcinctus*; Hhy- *Hydrochoerus hydrochaeris*; Lgy- *Lycalopex gymnocercus*. Note the different values on Y-axis.

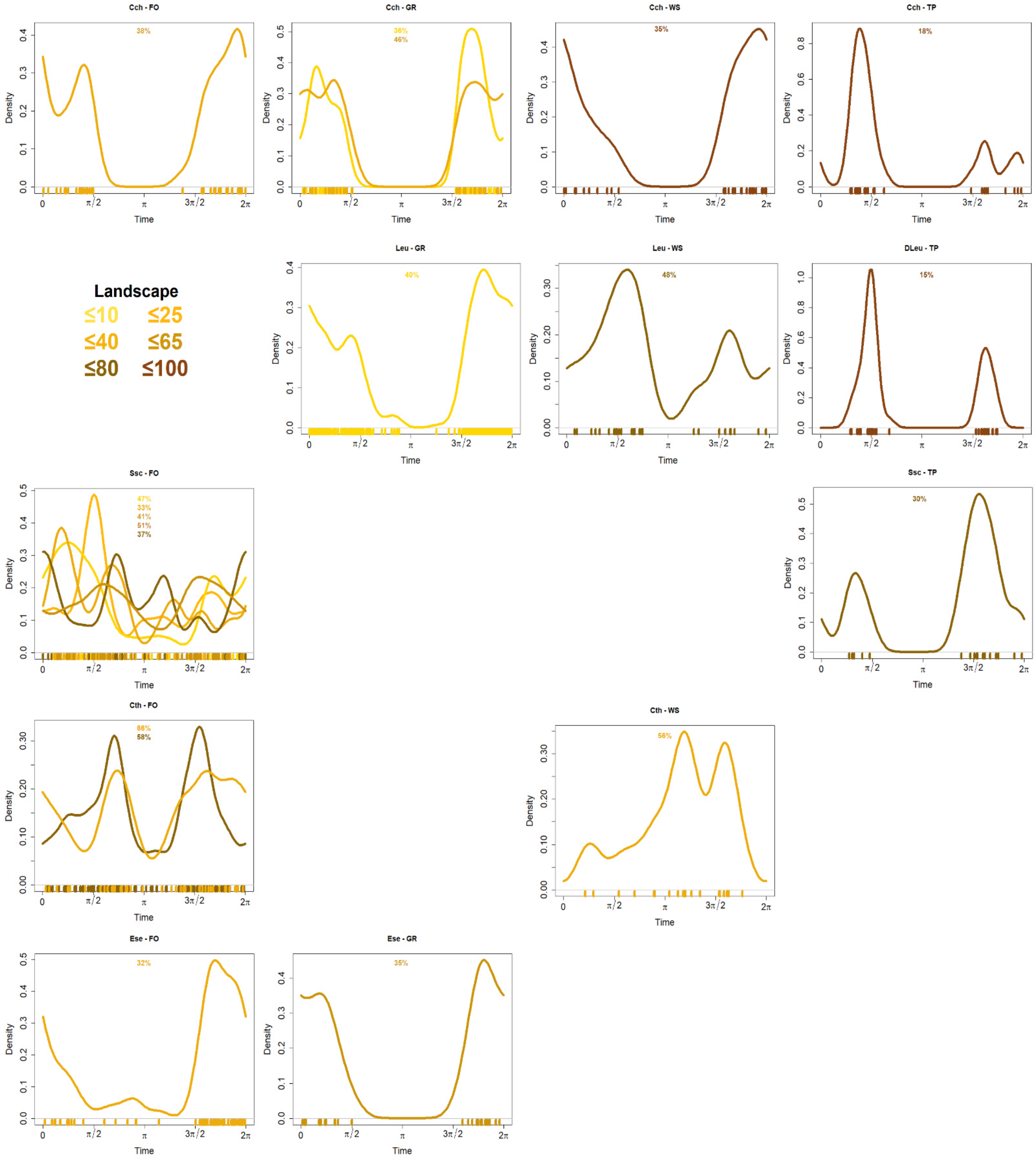

Fig. S4 (cont.) Density curve of activity patterns for species according to landscapes (≤10, ≤25, ≤40, ≤65, ≤80, and ≤100% TPC) and habitat types (Forest -FO-, Wooded Savanna -WS-, Grassland -GR-, Tree Plantation -TP-). Sun-time positions are as follows: 3π/2 = sunset, 0 = midnight, π/2 = sunrise, and π = solar noon. Habitat types are displayed as columns and species as rows. Species are identified by acronyms. References: Cth- *Cerdocyon thous*; Cch- *Conepatus chinga*; Ese- *Euphractus sexcinctus*; Leu- *Lepus europaeus*; Ssc- *Sus scrofa*. Note the different values on Y-axis.

According to the habitat types, there were significant differences for 7 of 9 species registered in more than one habitat (**Table S3**). Differences within habitats are shown in **Table S4**.

Table S4 Between habitat pairs comparison of species daily activity patterns (Forest -FO-, Wooded Savannah -WS-, Grassland-GR-, Tree Plantation -TP-). Values shown represent: Mann-Whitney p-values considering each species in each habitat activity level (Act) and percentage of night records (%Night). Significant p-values (<0.05) are shown in bold. Species are identified by acronyms and silhouettes -vectorized from (De Angelo *et al.* 2017) and authors photographs-. References: Aax: *Axis axis*; Cth: *Cerdocyon thous*; Cch: *Conepatus chinga*; Dno: *Dasypus novemcinctus*; Ese: *Euphractus sexcinctus*; Hhy: *Hydrochoerus hydrochaeris*; Leu: *Lepus europaeus*; Lgy: *Lycalopex gymnocercus*; Ssc: *Sus scrofa*.

Habitat types		**Species daily activity patterns differences**								
		Aax 	***Cth*** 	***Cch*** 	***Dno*** 	***Ese*** 	***Hhy*** 	***Leu*** 	***Lgy*** 	***Ssc*** 
GR-FO	**Act**	**0.002**	**0.031**	0.897	0.847	0.826	0.478	-	0.798	-
	%Night	**0.003**	**0.023**	0.145	0.187	0.349	0.623	-	**0.005**	-
GR-WS	**Act**	**0.008**	**0.039**	0.586	0.478	0.761	0.298	**0.041**	**0.045**	-
	%Night	**0.020**	**0.045**	0.298	0.398	0.467	**0.049**	**0.023**	**0.018**	-
GR-TP	**Act**	0.875	-	**0.022**	0.632	-	-	**0.048**	**0.049**	-
	%Night	**0.006**	-	**0.016**	0.089	-	-	**0.003**	**0.023**	-
FO-WS	**Act**	**0.034**	0.389	0.764	0.687	0.873	**0.061**	-	**0.032**	**0.018**
	%Night	0.209	0.053	0.564	0.287	0.379	**0.041**	-	**0.009**	**0.038**
FO-TP	**Act**	**0.001**	-	**0.009**	0.789	-	-	-	**0.050**	**0.013**
	%Night	0.783	-	**0.047**	0.092	-	-	-	**0.002**	**0.046**
WS-TP	**Act**	**0.009**	-	**0.012**	0.831	-	-	**0.021**	**0.031**	0.698
	%Night	0.308	-	**0.049**	0.099	-	-	**0.035**	**0.007**	**0.048**

Appendix IV – Lunar activity patterns

When day records were enough, night and day activity according to the moon phases was analyzed for each species and habitat type. This analysis was performed for the species with cathemeral, mostly nocturnal and nocturnal activity patterns (**Fig. S5**).

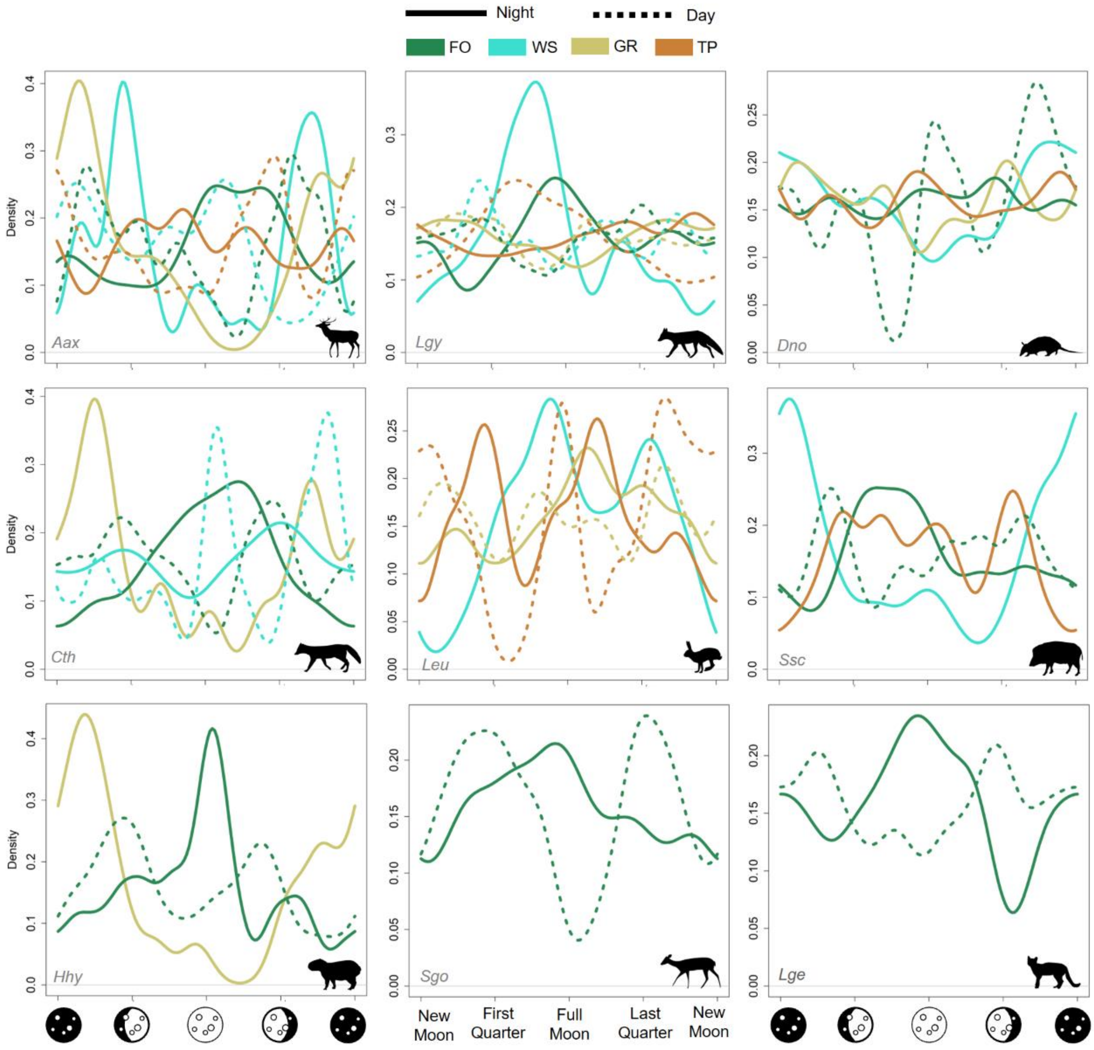

Fig. S5. Moon activity patterns for species recorded different habitat types (Forest -FO-, Wooded Savannah -WS-, Grassland -GR-, Tree Plantation -TP-) considering daytime (dotted lines) and nighttime (solid lines). Moon-phases are shown in the X-axis as followed: $\mathbf{0}$ = New Moon, $\boldsymbol{\pi/2}$ = First Quarter, $\boldsymbol{\pi}$ = Full Moon, and $\boldsymbol{3\pi/2}$ = Last Quarter; Habitat types are displayed with different colors. Species are identified by silhouettes -vectorized from (De Angelo *et al.* 2017) and authors photographs- and Latin names. Note the different values on Y-axis.

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Ampliación de la distribución del Margay *Leopardus wiedii* (Mammalia: Carnivora: Felidae) en Uruguay

NOTA

AMPLIACIÓN DE LA DISTRIBUCIÓN DEL MARGAY *Leopardus wiedii* (MAMMALIA: CARNIVORA: FELIDAE) EN URUGUAY

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RESUMEN

Se reporta una nueva localidad para *Leopardus wiedii* en Uruguay, en base a un registro fotográfico obtenido con una cámara trampa en el departamento de Flores. Se amplía la distribución conocida de la especie 150 km hacia el Oeste en el territorio uruguayo y se registra por primera vez en la cuenca del río Yi.

Palabras Clave: Felidae, nuevo registro, paisaje agroforestal, corredores biológicos.

ABSTRACT

Extension of the distribution range of margay *Leopardus wiedii* (Mammalia: Carnivora: Felidae) for Uruguay. We report a new location for *Leopardus wiedii* (margay) in Uruguay, based on photographs taken by a camera-trap in Flores department, which extend the known distribution range for the specie 150km to the West and constituted the first record in the Yi river basin.

Keywords: Felidae, new record, agroforestry landscape, biological corridors.

El margay (*Leopardus wiedii*) es un mamífero que pertenece al Orden Carnivora y la familia Felidae. Su distribución es casi exclusivamente Neotropical, extendiéndose desde el norte de Texas (Estados Unidos) por América Central, Venezuela, Colombia, Ecuador, Bolivia, Brasil, este de Perú, sureste de Paraguay, hasta el norte de Argentina y este de Uruguay (Oliveira, 1998; González & Martínez-Lanfranco, 2010).

Habita principalmente regiones tropicales y subtropicales y muestra una asociación con hábitats boscosos mayor que la de cualquier otra especie de felino americano (Oliveira, 1998; González & Martínez-Lanfranco, 2010). Su cuerpo se encuentra adaptado a la vida arbórea, presentando extremidades posteriores capaces de rotar 180º, lo que le permite descender cabeza abajo de los árboles, y cola proporcionalmente larga y ancha empleada para ayudar a mantener el equilibrio en las ramas (Oliveira, 1998). A pesar de que también se desplaza y caza en el suelo, descansa exclusivamente en lo alto de los árboles (Carvajal-Villareal *et al.*, 2012; Oliveira *et al.*, 2015).

A nivel internacional se cataloga como Cercano a la Amenaza (NT: Near Threatened) según la UICN (Unión Internacional para la Conservación de la Naturaleza). Sus poblaciones se encuentran en disminución como consecuencia de la transformación y fragmentación de hábitats boscosos para distintas actividades antrópicas, junto con la caza furtiva (González & Martínez-Lanfranco, 2010; Oliveira *et al.*, 2015). A nivel nacional se considera una especie Vulnerable y rara (Soutullo *et al.*, 2013), debido a que es especialista de hábitat, y presenta poblaciones pequeñas cuyo tamaño y distribución han disminuido significativamente en el tiempo (González & Martínez-Lanfranco, 2010; Soutullo *et al.*, 2013). En función de esto, ha sido catalogada como especie prioritaria para la conservación en el país y es considerada en el diseño del Sistema Nacional de Áreas Protegidas (SNAP) (Soutullo *et al.*, 2013).

En Uruguay, los registros de *L. wiedii* se agrupan en la franja este del país. Abarcan partes de los departamentos de Cerro Largo, Durazno, Lavalleja, Treinta y Tres, Maldonado, Rocha, Rivera y Tacuarembó (Fig. 1). Mediante modelos de distribución potencial para Uruguay, Bou (2013) determinó que las zonas de mayor idoneidad de hábitat para esta especie coinciden con las sierras del Sur en Maldonado y Rocha, continuando por la cuchilla Grande a través de Lavalleja y Treinta y Tres. Es en estas zonas donde efectivamente se concentran la mayoría de los registros, que coinciden con un área donde existen grandes extensiones de bosque serrano y de quebrada (Panario *et al.*, 2015), hábitats favorables para la especie (González & Martínez-Lanfranco, 2010). El área de distribución potencial incluye también paisajes dominados por praderas, pero surcados por sistemas de bosques ribereños, bañados y pajonales asociados a ríos y arroyos, que podrían constituir corredores ecológicos (Bou, 2013). La distribución potencial podría alcanzar con menor probabilidad Montevideo, Canelones, San José y Florida (Bou, 2013: Fig. 1).

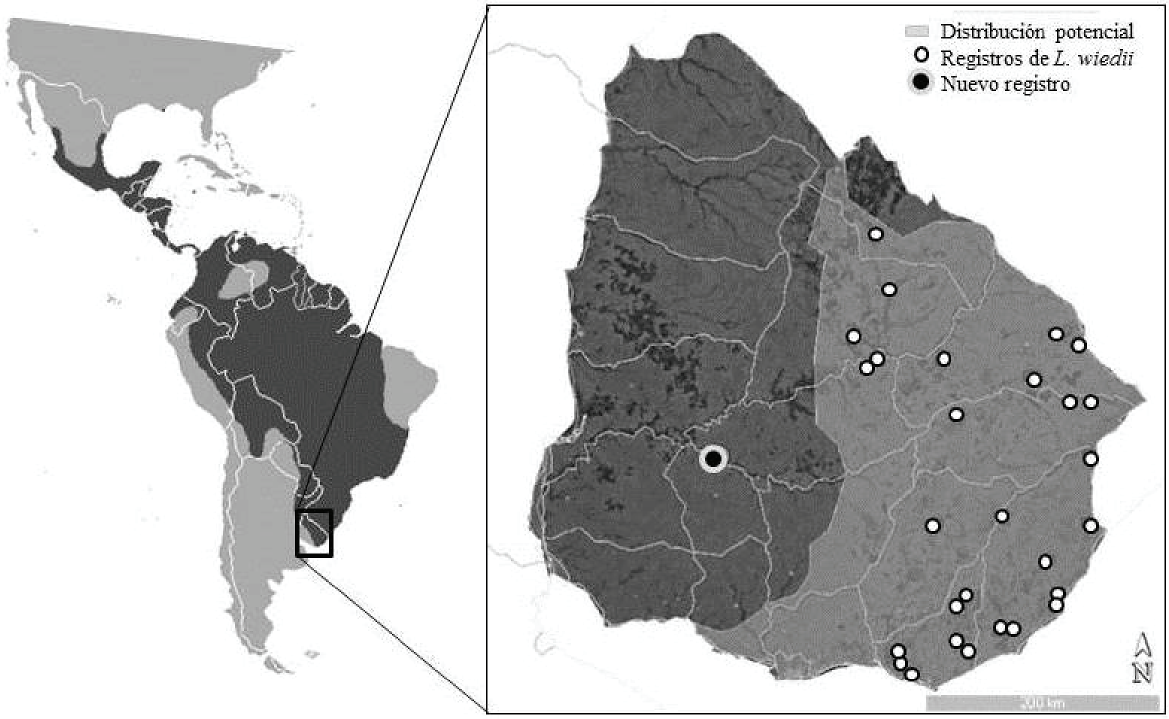

Fig. 1. Rango de distribución de *L. wiedii* (Wilson & Mittermeier, 2009), área de distribución potencial en Uruguay, registros previos (Bou, 2013) y nuevo registro.

La presente nota tiene como objetivo reportar una nueva localidad de registro para *L. wiedii*, que representa la ampliación del área de distribución conocida para la especie (Fig. 2). Los autores han desarrollado trabajos de monitoreo de mamíferos mediante el uso de cámaras trampa (StealthCam G42NG) en establecimientos agroforestales del litoral oeste y centro del país pertenecientes a la empresa Montes del Plata. En enero de 2016 se obtuvieron fotografías de un ejemplar de *L. wiedii* en el departamento de Flores (Establecimiento Los Arroyos), durante horas de la noche (Fig. 2).

Esta nueva localidad se encuentra a 150 km al Oeste del registro conocido más cercano de la especie. El espécimen fue registrado en una zona de bosques nativos con roquedales, aledaños al bosque ribereño del río YÍ. Los principales usos de la tierra en la zona de registro, son el agroforestal (plantaciones de *Eucalyptus* sp. para producción de pulpa de celulosa) y ganadero (con presencia de ganado bovino, ovino y equino). A pesar de las actividades antrópicas, el bosque se encontraba en buenas condiciones: presentaba árboles fustales de alto porte, no se constató la presencia de especies exóticas ni evidencia de talas recientes. Simultáneamente, se registraron en esta área otras 10 especies de mamíferos de mediano/gran porte y 11 de pequeño porte, así como una considerable riqueza de aves, anfibios y reptiles. Varios estudios han demostrado que ésta especie es muy sensible a los disturbios antrópicos, en comparación con otros félidos pequeños (Vaughan, 1983; Mondolfi, 1986; Tello, 1986; Azevedo, 1996). Sin embargo, también ha sido detectada en paisajes parchados y agroforestales, siempre y cuando exista una cobertura arbórea mínima (Vaughan, 1983; Mondolfi, 1986; Tello, 1986; Oliveira *et al.*, 2010, 2015), como aparenta ocurrir en esta localidad. Sin embargo, se debería monitorear el área por más tiempo, para determinar si la presencia de la especie fue un fenómeno anecdótico, o es algo más estable.

Agradecemos a los dos revisores anónimos con cuyos aportes se mejoró sustancialmente el manuscrito. A Lic. Federico Haretche y Msc. Verónica Etchebarne por su participación y apoyo durante los muestreos de campo y trabajo de gabinete. A la empresa forestal Montes del Plata (MDP), por permitir el acceso a sus predios y por el apoyo logístico. Particularmente apreciamos el apoyo del encargado del área ambiental de MDP, Ing. Agr. For. Horacio Giordano, y la colaboración del encargado del

Fig. 2. Fotografía del ejemplar de *Leopardus wiedii* registrado en el departamento de Flores.

Establecimiento Los Arroyos, Ing. Agr. For. Alejandro Fros, y de los caseros Nicolás y Camila. Este trabajo fue financiado en parte por el Proyecto de Iniciación (INI_X_2013_1_101221) y Beca de Maestría Nacional (POS_NAC_2015_1_109965) de la Agencia Nacional de Investigación e Innovación, otorgados a AC, y por el Proyecto CSIC I+D VSUP dirigido por AB.

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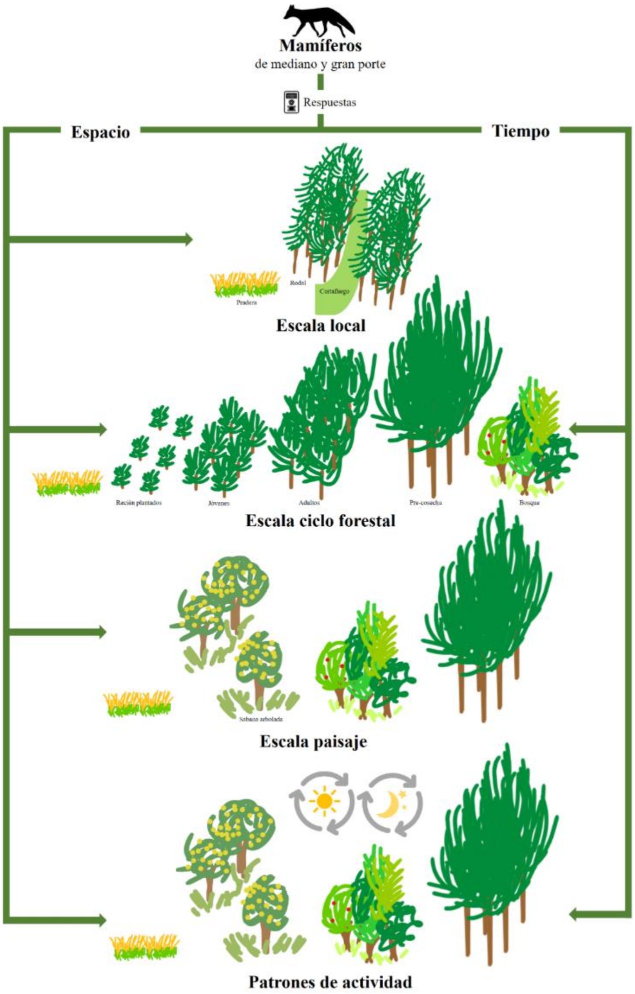
Fecha de Aceptación: 10 de mayo de 2017

5. Discusión y conclusiones generales



5. Discusión y Conclusiones generales

Entre 2015 y 2021 fueron registradas 19 especies de mamíferos de mediano y gran porte. De ellas, 14 correspondieron a especies nativas (*Cerdocyon thous*, *Conepatus chinga*, *Dasypus septemcinctus*, *Dasypus novemcinctus*, *Didelphis albiventris*, *Euphractus sexcinctus*, *Galictus cuja*, *Hydrochoerus hydrochaeris*, *Leopardus geoffroyi*, *Leopardus wiedii*, *Lontra longicaudis*, *Lycalopex gymnocercus*, *Procyon cancrivorus*, *Subulo gouazoubira*), 2 fueron especies reintroducidas dentro de las áreas de estudio (*Nasua nasua*, *Pecari tajacu*) y finalmente 3 exóticas (*Axis axis*, *Lepus europaeus*, *Sus scrofa*). Los patrones tanto espaciales como temporales de las mencionadas especies fueron evaluados a lo largo de los distintos capítulos presentados como artículos científicos.

Efectos espacio-temporales

Los cambios en la configuración del paisaje pueden provocar tanto modificaciones en la composición de los ecosistemas como en la diversidad de especies que los habitan al afectar sus patrones tanto espaciales como temporales a distintas escalas (Liu and Andersson 2004; Norris et al. 2010; Wong and Candolin 2015; Iglesias-Carrasco et al. 2022; Liu et al. 2022). Estas respuestas, no son constantes ni uniformes para todas las especies sino más bien especie-específicas y paisaje-específicas, pudiendo ser positivas, negativas o incluso neutras, siendo sus características y requerimientos biológicos los que influyen sobre el tipo de respuesta, incluso sobre su presencia o ausencia en el sitio (Lindenmayer and Hobbs 2004; Carnus et al. 2006; Fischer and Lindenmayer 2006; Pawson et al. 2008; Bilenca et al. 2017), como se irá viendo a continuación.

A lo largo de los artículos derivados de la presente tesis de doctorado, distintas respuestas por parte de mamíferos ante predios forestados pudieron ser observadas a distintas escalas tanto espaciales como temporales. De estos estudios, dos resultados consistentes se destacan: (1) los paisajes forestados de Uruguay no son “desiertos verdes” (áreas sin especies), ya que varias de especies de mamíferos hacen uso de este "neoecosistema”; (2) estos ensambles de mamíferos en estos paisajes forestados son distintos a los que se desarrollan en ecosistemas nativos, presentando una menor diversidad de especies, mayor dominancia de especies generalistas, y en segundo lugar, de especialistas de bosque y la ausencia de especialistas de pastizal.

Esta tendencia de paisajes forestales dominados por generalistas de hábitat y algunos especialistas de bosque, disminuyendo significativamente la presencia de especialistas de pastizal, se ha visto en otros trabajos sobre mamíferos regionales (Martin et al. 2012; Timo et al. 2015; Brazeiro et al. 2018; Iezzi et al. 2020, 2021; Almeida-Maués et al. 2022), y en otros grupos animales como mariposas (da Rocha et al. 2013; Casas-Pinilla et al. 2022), hormigas (Martello et al. 2018), reptiles (da Rocha et al. 2013; da Silva Alves Saccol et al. 2017) y aves (Dias et al. 2013; Jacoboski et al. 2016; Phifer et al. 2017;

Vaccaro et al. 2019; Jacoboski and Hartz 2020; Martínez-Lanfranco et al. 2022), pero también en trabajos de composición de plantas (Pairo et al. 2021). Las especies generalistas tienen una mayor tolerancia a “nuevos hábitats” forestados al presentar una mayor plasticidad comportamental ante la disponibilidad de recursos (da Silva 2001; da Silveira 2005; Lyra-Jorge et al. 2008; Andrade-Núñez and Aide 2010; Dotta and Verdade 2011; O’Callaghan et al. 2016; Mosquera-Guerra et al. 2018; Iezzi et al. 2020, 2021; Iglesias-Carrasco et al. 2022). Ante y a pesar ello, se puede decir que las plantaciones forestales no constituyen un “desierto verde” (*sensu* Bremer and Farley 2010), siempre cuando persistan ecosistemas nativos en los paisajes, siendo que el 70% de las especies registradas en los paisajes forestales estudiados hacen uso de alguna u otra forma de los componentes de las plantaciones de *Eucalyptus*, no identificándolas como una barrera. Pero no todo cambio o adaptación en las especies presentes es positivo. Estas tendencias observadas en cuanto a composición de especies en paisajes forestales pueden ser interpretadas como una homogenización espacial del comportamiento de las especies (Iglesias-Carrasco et al. 2022).

En lo que refiere a las especies de bosque, a pesar de que se asume que las plantaciones de *Eucalyptus* podrían llevar a favorecerlas por ser fisonómicamente más parecidos a bosques que a los pastizales que formaban parte de la matriz ambiental original, los registros obtenidos en esta tesis mostraron mayores registros de especies de bosque en pastizales remanentes que en parches forestados recientemente -Edad 1-, adultos -Edad 3- o maduros -Edad 4-. Sin embargo, los cortafuegos, considerados transectos lineales sin cultivar que se encuentran entre los rodales cultivados, fueron utilizados en gran medida por especies especialistas de bosque y generalistas, y en relación con gremios tróficos, por carnívoros, omnívoros e insectívoros. Los cortafuegos, así como otros tipos de estructuras lineales, son utilizados por los mamíferos para circular de forma más eficiente dentro de los paisajes. Así como en este estudio, en la región este patrón ha sido observado en Argentina (Lantschner 2012; Decarre 2015), Chile (McFadden and Dirzo 2018) y Brasil (da Silva 2001; da Silveira 2005; Timo et al. 2015). Estos hallazgos de uso espacial de los cortafuegos, sumado al uso temporal observado (acotado en comparación con ambientes nativos), sugiere el rol potencial de estos como corredores y/o conectores entre vegetación nativa remanente.

Cuando un determinado ambiente se ve disminuido, la riqueza y abundancia de las especies así como el intercambio genético entre poblaciones puede verse disminuido también (Moreno and Guerrero-Jimenez 2019). Ante ello, los corredores biológicos son una de las principales herramientas promovidas para procurar la conservación de la biodiversidad en paisajes fragmentados y/o modificados (e.g. González-Maya et al. 2013; Moreno and Guerrero-Jimenez 2019). Se enfatiza entonces el papel que los cortafuegos pueden tener en paisajes forestales y por ende la importancia de su planificación y diseño, más allá de las reglamentaciones nacionales para mitigación de incendios. Este uso diferencial entre los dos componentes forestales evaluados, rodales maduros y cortafuegos, derivó en que los resultados hayan indicado que son significativamente diferentes tanto en riqueza, como en composición e intensidad de uso por parte de mamíferos de mediano y gran porte.

En plantaciones jóvenes -Edad 2-, sin embargo, los rodales forestales pasan a ser ampliamente utilizados por diversas especies registradas a lo largo de los monitoreos. Los *Eucalyptus* varían significativamente a lo largo del ciclo productivo, sobre todo en lo que refiere a la fisonomía de la vegetación (Santoandré et al. 2021). Tras la preparación del suelo, se plantan árboles híbridos provenientes de viveros, los cuales crecen generando una estructura de arbustos, pasan una etapa intermedia de estructura más boscosa con ramas bajas y sotobosque, hasta alcanzar una etapa de árboles de gran altura con vegetación baja muy reducida (Turnbull 1999; Wagner et al. 2006; Tomé et al. 2021). Durante la etapa intermedia (i.e., plantaciones jóvenes -Edad 2-), la estructura de la vegetación mostró semejanza con la estructura de los bosques nativos, resultando en una gran similitud del ensamble de mamíferos presente, como también se ha visto en otros trabajos de la región (Timo et al. 2015). La hipótesis de heterogeneidad de hábitat (Simpson 1949; MacArthur and Wilson 1967) establece que aquellos hábitats estructuralmente más complejos (i.e., bosques y plantaciones jóvenes), ofrecen más nichos para mantener mayor diversidad que hábitats más homogéneos.

Las similitudes y diferencias en riqueza de especies entre las diferentes etapas del ciclo respondieron únicamente a factores locales, coincidiendo con planteos de Wearn y colaboradores (2019), quienes plantean que la influencia del paisaje disminuye a medida que el uso del suelo se intensifica y entonces las variables locales vinculadas a la estructura del hábitat ganan fuerza. Sin embargo, al incorporar la identidad de las especies, tanto los factores locales como los del paisaje incidieron en los resultados encontrados. A lo largo del ciclo, las condiciones contrastantes de las distintas etapas mostraron ser importantes filtros de la composición de especies, pero también las distancias a los ecosistemas boscosos, posiblemente vinculado a la capacidad de dispersión de las especies y a los distintos procesos (e.g., forrajeo, reproducción, reposo) que llevan a cabo dentro de los componentes del paisaje (Addicott et al. 1987; Jackson and Fahrig 2012, 2015; Tscharntke et al. 2012; Driscoll et al. 2013; Wearn et al. 2019; Riva and Nielsen 2020). A escala paisaje, estas variables fueron también seleccionadas como significativas en este trabajo y en otros de la región (Iezzi et al. 2021). La cercanía y/o porcentaje de bosque en la vecindad, como factores determinantes, ponen en evidencia la escala del efecto paisaje (i.e., scale of effect en inglés), que en nuestro caso se focalizó en el entorno cercano (5km a nivel de paisaje, 500m y 1km a nivel de estación de muestreo) en el registro de especies (Jackson and Fahrig 2012, 2015; Wearn et al. 2019). Ante esto, se destaca sobre todo la ausencia de significancia en el efecto de la superficie forestada sobre la riqueza y composición del ensamble de mamíferos, salvo en el caso de las plantaciones localmente, donde el entorno nativo es clave. Varios trabajos de paisajes forestales han resaltado la importancia de los parches naturales para el mantenimiento de especies dentro del paisajes y dentro de las plantaciones propiamente dichas, al aumentar la heterogeneidad ambiental (Lindenmayer and Hobbs 2004; Fischer and Lindenmayer 2007; Lindenmayer et al. 2015; Iezzi et al. 2019). Los bosques, para aquellas especies especialistas de estos ambientes, así como para las generalistas, podrían estar actuando como fuente, pudiendo ser identificados como "estructuras clave" ("keystone structures" en inglés, i.e., estructuras espaciales que proveen de recursos o refugios esenciales para las especies, *sensu* (Tews et al. 2004). En este sentido, las plantaciones jóvenes -Edad 2- podrían estar brindando recursos adicionales para las especies que hacen uso de estos ambientes al ser estructuralmente más complejos que edades de plantación más tempranas o tardías -Edades 1, 3 y 4-.

Pero ¿qué ocurre con los especialistas de pradera? Mientras que los bosques cercanos no incidieron en su riqueza, abundancia o composición, si lo hicieron los remanentes de pastizal existentes. La superficie de pradera (5km a nivel de paisaje, 500m a nivel de estación de muestreo), fue relevante tanto en la composición de especies general como en la riqueza dentro de las estaciones de muestreo de ese mismo ambiente. Puntualmente, la cantidad de pastizal remanente a pequeña escala (500m), posiblemente vinculada a la capacidad de movimiento de las especies para cumplir sus requerimientos ecológicos (Jackson and Fahrig 2012, 2015; Wearn et al. 2019), explicó significativamente la presencia y frecuencia de especialistas de pradera como la mulita (*D. septemcinctus*), que estuvo ausente tanto en rodales como en cortafuegos.

La mulita, es considerada tanto un especialista de hábitat como de dieta (Abba et al. 2011, 2015), siendo más sensible a los cambios que otros armadillos (i.e., *D. novemcinctus*). En este contexto, era esperable que los especialistas sean las especies más susceptibles a la pérdida y fragmentación de hábitat (Fahrig 2003; Jackson and Fahrig 2012). En apoyo a esta hipótesis, una revisión de los efectos de los cambios de uso y cobertura del suelo sobre la biodiversidad, encontró que los especialistas de hábitat y los mamíferos de baja dispersión y/o ámbito de hogar, tienen probabilidades mucho más reducidas de ocurrencia en hábitats modificados a nivel mundial (e.g. Newbold et al. 2014).

Considerando que la mulita podría ser la especie de mamífero más amenazada por la conversión de pastizales naturales en monocultivos en Uruguay (Andrade-Núñez and Aide 2010; Abba et al. 2016; Bilenca et al. 2017), determinar umbrales de tolerancia a la pérdida de hábitat para la especie cobra importancia. Los umbrales, definidos por puntos de inflexión, son intervalos de transición a través de los cuales pequeños cambios en el patrón espacial producen cambios abruptos en las respuestas ecológicas (Turner and Gardner 1991; With and Crist 1995; Fahrig 2003; Ewers and Didham 2006; Swift and Hannon 2010; Thompson 2011). Los posibles umbrales vinculados a la cobertura de pastizal a escala paisaje fueron determinados dentro de un entorno de 5km: en paisajes con menos de

70% de pradera remanente, los especialistas como la mulita comienzan a ser menos frecuentes, y al alcanzar el 40%, se pierden.

Desde el punto de vista temporal, mientras el contexto paisaje no afectó los patrones horarios de las especies, si lo hizo el tipo de hábitat en cual las cámaras trampa estaban insertas. En relación con el ciclo solar diario, dentro de ambientes modificados, generalmente la actividad diurna representa una barrera para el movimiento entre y hacia hábitats favorables (Daily and Ehrlich 1996; Donati and Borgognini-Tarli 2006; Wong and Candolin 2015), mientras que la catemeralidad (i.e., metaturnalidad) se hace más frecuente al permitir más plasticidad en el rango temporal de actividad (Norris et al. 2010; Bennie et al. 2014) y la nocturnidad, al reducir fuentes de amenaza (Bennie et al. 2014; Muñoz-García et al. 2018; Gaynor et al. 2019). Por otro lado, así como existen vínculos con la posición solar, también los hay con las fases de la luna. ¿Será que la nocturnidad siempre reduce amenazas? El ciclo lunar, pasando de luna llena a luna nueva, afecta la luminosidad entre otros factores, los cuales también determinan el comportamiento de las especies bajo dichas condiciones (Bennie et al. 2014; Pratas-Santiago et al. 2016; Botts et al. 2020a, b).

Coincidentemente, los patrones catemerales y nocturnos fueron los dominantes entre las especies presentes en los paisajes forestales. Por el contrario, la mulita, además de ser afectada por el porcentaje de forestación, fue también la única especie con actividad exclusivamente diurna. Estas tendencias observadas pueden ser interpretadas como una homogenización temporal del comportamiento de las especies (Iglesias-Carrasco et al. 2022). El tipo de hábitat relevado, y por ende su cobertura, influyó en los patrones observados. Se observaron tendencias claras de uso de áreas abiertas en horas de la noche, así como en luna nueva y, por el contrario, en áreas con cobertura vegetal mayor, durante horas del día y luna llena. Estos patrones de uso temporal en relación con la cobertura vegetal se ha visto en otras trabajos (Preisler et al. 2006; Godvik et al. 2009; Gaynor et al. 2019, 2021; Botts et al. 2020b; Richter et al. 2020). Dentro de las plantaciones forestales de *Eucalyptus*, tanto los cortafuegos como los rodales mostraron el mismo uso temporal (a diferencia de lo observado desde el punto de vista espacial) para aquellas especies registradas en ambos. Como fue mencionado anteriormente, los momentos de actividad fueron más acotados que en el caso de los ambientes nativos, donde los patrones de actividad mostraron más continuidad temporal, salvo en el caso de especies más generalistas como *D. novemcinctus* y *E. sexcintus* que presentaron actividad constante sin importar el tipo de hábitat. Algunas especies aumentaron los registros diurnos en comparación al ritmo de actividad registrado en áreas abiertas (pastizales y sabanas arboladas), asimilándose al patrón que presentaron en bosques (*A. axis*, *C. chinga*), otras aumentaron los registros nocturnos (*L. gymnocercus*) o se mantuvieron constantes temporalmente (*L. europaeus*, *S. scrofa*). Similares patrones se observaron para diversas especies con la luna (*L. gymnocercus, A. axis, C. thous, S. scrofa, E. sexcinctus, H. hydrochaeris, L. geoffroyi, S. gouazoubira* and *P. cancrivorus*):

áreas abiertas en luna nueva, áreas cerradas en luna llena. Las tendencias de luno-fobia (menor actividad en luna llena), ya se habían observado en diversas especies que reducen el uso de ambientes abiertos o donde la luminosidad lunar puede atravesar fácilmente (Morrison 1978; Gilbert and Boutin 1991; Kotler et al. 1991; Saldaña-Vázquez and Munguía-Rosas 2013; Prugh and Golden 2014), y contrariamente tendencias de luno-filia (mayor actividad en luna llena) en áreas cubiertas (Karlsson et al. 2002; Gursky 2003; Michalski and Norris 2011; Saldaña-Vázquez and Munguía-Rosas 2013), pero no para todas las especies (Pratas-Santiago et al. 2016, 2017; Botts et al. 2020a). Esto demuestra distintas adaptaciones a los cambios en ambientes disponibles dentro del paisaje, especie-específicas, y son varios los factores interconectados que se podrían explicar dichas tendencias.

Uno de ellos refiere al compromiso que deben hacer las especies entre la presión de caza y/o depredación con la alimentación (Iglesias-Carrasco et al. 2022). Por un lado los herbívoros, y otras especies presa, deben balancear la necesidad de forrajeo con la evasión de depredadores (Prugh and Golden 2014; Moll et al. 2017; Fattebert et al. 2019), y ese balance que deben alcanzar puede variar tanto en el espacio como el tiempo (Frey et al. 2017; Lone et al. 2017; Botts et al. 2020b, a). En ese sentido, áreas abiertas como pastizales y sabanas arboladas, ofrecen mayores recursos forrajeros (Hebblewhite et al. 2008; Godvik et al. 2009), mientras que las áreas de cobertura, como bosques y plantaciones, pueden representar protección ante depredadores (Fardell et al. 2021). Pero no sólo los herbívoros u otros animales presa evitan depredadores. Para carnívoros y diversas especies que sean objeto de caza, los humanos son percibidos como un riesgo (Stafford et al. 2017; Gaynor et al. 2019, 2021; Mendes et al. 2019; Carreira et al. 2020; Richter et al. 2020; Iglesias-Carrasco et al. 2022). Surge así el concepto de "paisaje del temor" (landscape of fear en inglés) (Dammhahn et al. 2022; Palmer et al. 2022), que no es una percepción constante sino dinámica tanto en el espacio como el tiempo, impulsando una mayor nocturnidad en las especies (Bennie et al. 2014; Gaynor et al. 2019; Iglesias-Carrasco et al. 2022), o en áreas cubiertas para reducir encuentros con humanos (Little et al. 2016; Gaynor et al. 2018; Richter et al. 2020), o en áreas abiertas durante fases lunares de baja luminosidad (Morrison 1978; Gilbert and Boutin 1991; Kotler et al. 1991; Saldaña-Vázquez and Munguía-Rosas 2013), o directamente evitar áreas por completo (Carter et al. 2012; Tucker et al. 2018). La percepción de riesgo por parte de las especies podría entonces tener importantes efecto sobre las interacciones entre las especies tanto en el espacio como en el tiempo (Laundré et al. 2001, 2010; Gaynor et al. 2019) dependiendo de movimientos humanos, ruidos, luz, cobertura vegetal, entre otros (Verdolin 2006). Desde el punto de vista espacio-temporal, las etapas de la plantación podrían mostrar distintos niveles de riesgo para las especies en este sentido de evasión de amenazadas: durante las primeras -Edad 1- y últimas etapas -Edad 4- la baja vegetación podría afectar negativamente, mientras que en etapas jóvenes -Edad 2- e intermedias -Edad 3- presentan estructura de sotobosque y cobertura herbácea ofreciendo tanto disponibilidad de forrajeo como percepción de “seguridad”, coincidiendo con los patrones observadores durante el ciclo evaluado.

Como mencionado previamente, la luminosidad es un factor relevante en la selección de comportamientos tanto espaciales como temporales por parte de las especies (Fernandez-Duque and Erkert 2006; Fernández-Duque et al. 2010; Gerkema et al. 2013; Prugh and Golden 2014; Pratas-Santiago et al. 2017; Wu et al. 2017; Botts et al. 2020a; Gaynor et al. 2021), afectada por la cobertura de nubes, por el sol, por la luna, por la cobertura vegetal, pero también de la agudeza visual propia de las mismas especies, vinculada a la presencia de *tapetum ludicum* -capa de tejido ubicada en la parte posterior del ojo de diversos vertebrados que actúa como un espejo que refleja los rayos luminosos, mejorando la visión en condiciones de escasa luminosidad- (Schwab et al. 2002; Ollivier et al. 2004; Prugh and Golden 2014; Pratas-Santiago et al. 2017; Botts et al. 2020a).

Recomendaciones de manejo

Las modificaciones en el paisaje pueden afectar significativamente a especies especialistas, mientras que aquellas generalistas pueden ser temporalmente beneficiadas a lo largo del ciclo forestal. La pérdida de especialistas puede derivar a una homogenización del ensamble de mamíferos tanto en el espacio como en el tiempo, por lo que diversas acciones de manejo a ser implementadas pueden generar mayor heterogeneidad en los paisajes que permita enriquecer el ensamble de especies:

(1) establecer mayor separación entre líneas de plantación para fomentar la permanencia de vegetación herbácea y sotobosque al pasar más luz;
(2) planificar de rodales con distinta edad de plantación a lo largo del paisaje (considerando que plantaciones de edades heterogéneas aumentarían la diversidad de mamíferos del paisaje y proporcionarían más recursos para el mantenimiento de especies generalistas y de bosque);
(3) mantener parches de pastizal, además de bosques, que permitan funcionar como fuentes de especies y como “stepping stones” asociado al (4) diseño adecuado de la rodalización (i.e., definición de rodales que tendrá la plantación) y cortafuegos (destacando su rol como potenciales corredores) en el paisaje que promuevan la conectividad.
(4) considerar el patrón de actividad diario de las especies en relación con el sol y la luna, de forma tal de sincronizar las actividad de manejo para evitar el solapamiento con los picos de actividad de las especies, reduciendo así potenciales afectaciones al comportamiento de las mismas.

Puntalmente para especies especialistas de pastizal, como *D. septemcinctus*, medidas específicas deben enfatizarse teniendo en cuenta los umbrales de tolerancia detectados, teniendo en cuenta que se trata de las más amenazadas por actividades de cambios de uso y cobertura el suelo a lo largo de los Pastizales del Río de la Plata.

La incorporación de estos y otros resultados dentro de las exigencias de la normativa nacional y de certificadoras de producción responsable (e.g. Consejo de Administración Forestal - FSC por su nombre en inglés: Forest Stewardship Council; Programa de Reconocimiento de Sistemas de Certificación Forestal- PEFC por su nombre en inglés: Programme for the Endorsement of Forest Certification) se considera relevante así como la evaluación de la configuración de los paisajes forestales en búsqueda de la integración de mundos productivos y naturales para alcanzar paisajes multifuncionales.

Dada la continuidad y expansión proyectada de la forestación en Uruguay, centrar los esfuerzos de investigación en comprender las respuestas espaciotemporales de las especies y cómo se las arreglan en estos paisajes modificados es vital para la conservación y la toma de decisiones adecuadas.

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Anexo

Anexo I

1. Descripción de los paisajes forestados y sus ambientes

Contenido

Paisajes forestados

Los predios forestales considerados para responder los distintos objetivos corresponden a predios de *Eucalyptus* para la producción de celulosa de la empresa forestal Montes del Plata (MDP). MDP fue fundada en Uruguay en 2009. Su patrimonio territorial está distribuido en trece departamentos del país dentro de la región centro y oeste del país (Figura 1-1). Abarca 134.000 ha forestadas y 87.500 ha de áreas naturales. Dentro de su política de gestión, estableció un compromiso para gestionar sus negocios de manera social, ambiental y económicamente responsable. En este marco, un 96% (212.902 ha) de las áreas bajo gestión de MDP ya cuentan con la certificación FSC de Manejo Forestal Responsable (Montes del Plata, 2019).

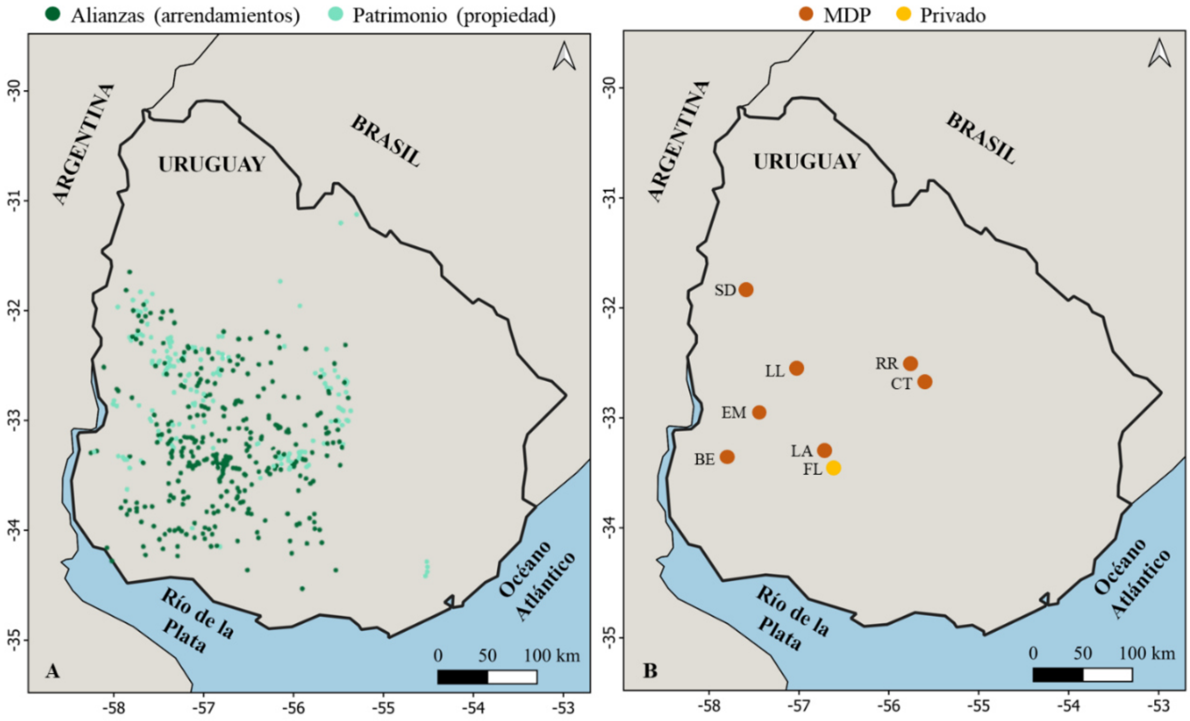

Figura 1-1. (A) Predios manejados por MDP (arrendamientos y propiedades); (B) Ubicación de las áreas de estudio.

Los inicios de este doctorado se enmarcan en una serie de convenios de cooperación entre MDP y Facultad de Ciencias ejecutados entre 2011 y 2017, con el objetivo de apoyar el desarrollo e implementación de una estrategia de conservación de la biodiversidad en predios forestales. Desde 2018 a 2021 los monitoreos fueron llevados a cabo por proyectos de investigación consiguientes. En los paisajes se analizaron todos los ambientes presentes, vegetación nativa y plantaciones: bosques cerrados – ribereño, serrano, pantanoso, con roquedales –, bosques abiertos – parques y parques arenosos –, praderas – baja, media, rocosa y alta – y plantaciones forestales de *Eucalyptus* para celulosa.

Dentro del patrimonio de MDP, fueron monitoreados 7 establecimientos cubriendo un gradiente de superficie forestada de 25 a 100% (Cueva del Tigre -CT-, Los Arroyos -LA-, Rincón del Río -RR-, Las Lilas -LL-, El Matorral -EM-, Santo Domingo -SD- y Bequeló -BE-) entre 2015 y 2021 (Figura 1-1). Por fuera de la empresa, se contó con un área de estudio control (Flores -FL-), sin forestación en el entorno de las restantes áreas (2021-2021) (Figura 1-1).

Detalle de las áreas de estudio

Establecimiento Los Arroyos -LA-

El área está ubicada en la región Norte del Departamento de Flores, en la costa del río Yí, próximo al Paraje Arroyo Malo, unos 35 km al Norte de Trinidad. Se encuentra ubicada en la eco-región Escudo Cristalino (Brazeiro, 2015).

Establecimiento Las Lilas -LL-

El área está ubicada en la región central del Departamento de Río Negro, adyacente a la Cuchilla de las Averías, próximo al Paraje Paso de Balbuena, unos 25 km al NW de Pueblo Grecco. Se encuentra ubicada en la eco-región Cuenca Sedimentaria del Oeste (Brazeiro, 2015).

Establecimiento El Matorral -EM-

El área está ubicada en la región Sur del Departamento de Río Negro, sobre la costa del río Negro, entre el Arroyo Don Esteban Grande y la Cañada del Sauce, próximo al Paraje Paso de los Cobres, unos 10 Km al Noroeste de Pueblo Palmar y unos 35 km al Sur de Young. Se encuentra ubicada en la eco-región Cuenca Sedimentaria del Oeste (Brazeiro, 2015).

Establecimiento Cueva del Tigre -CT-

El área está ubicada en la región noreste del Departamento de Durazno, sobre la Cañada del Tigre, próximo al paraje La Alegría y unos 15 km al nor-noreste de La Paloma. Se encuentra ubicada en la eco-región Cuenca Sedimentaria Gondwánica (Brazeiro, 2015).

Establecimiento Rincón del Río -RR-

El área está ubicada en la región noreste del Departamento de Durazno, sobre la costa del río Negro, unos 12 km al Oeste del paraje La Alegría y 23 km al nor-noroeste de La Paloma. Se encuentra en la eco-región Cuenca Sedimentaria Gondwánica (Brazeiro, 2015). El establecimiento presenta un Área de Alto Valor de Conservación (AAVC de ahora en más) que abarca una superficie de 424 has.

Establecimiento Santo Domingo -SD-

El área está ubicada en la región Sur del Departamento de Paysandú, con costa sobre el arroyo Guaviyú y dentro del área de distribución de los palmares de Yatay, próximo a la localidad de Quebracho (30km), unos 10 Km al oeste de Cerro Chato y 15 km del pueblo Gallinal. Se encuentra ubicada en la eco-región Cuenca Sedimentaria del Oeste (Brazeiro, 2015). El establecimiento presenta dos AAVC que abarcan una superficie de 80 has.

Establecimiento Bequeló y aledaños -BE-

El área está ubicada en la región Sur del Departamento de Soriano, sobre la costa del arroyo Bequeló, próximo al Paraje Cerro Alegre, unos 20 Km al Sureste de Mercedes. Se encuentra ubicada en la eco-región Cuenca Sedimentaria del Oeste (Brazeiro, 2015).

Establecimiento no forestado: Flores -FL-

El área está ubicada en la región Norte del Departamento de Flores, en la costa del río Yí, próximo al Paraje Arroyo Malo, unos 35 km al Norte de Trinidad, aledaño al establecimiento LA. Se encuentra ubicada en la eco-región Escudo Cristalino (Brazeiro, 2015). Se trata de un área no forestada dominada por pastizales.

Caracterización de ambientes

Dentro de cada paisaje, se llevaron a cabo relevamientos en terreno para la caracterización de los ambientes presentes. En el caso de las praderas, se llevó a cabo una caracterización estructural, considerando estratos y altura de estos. Con el fin de caracterizar la diversidad de especies leñosas y la estructura y fisonomía de los bosques nativos se realizaron relevamientos florísticos cualitativos y cuantitativos de los distintos tipos de bosque identificados en cada establecimiento.

En cada tipo de bosque, el componente arbóreo adulto se relevó en parcelas modificadas de Gentry de 0.1ha -5 transectas de 2x100m- (Boyle, 1996). En cada transecta se identificaron y midieron todos los individuos arbóreos adultos mayores o iguales a 2.5cm de DAP (diámetro a la altura del pecho, aprox. 1,3 m). Para cada individuo se anotó el estrato que ocupa en el bosque (sotobosque, dosel o emergente). Para todas las transectas se registró la posición topográfica, la orientación de la pendiente, las coordenadas y altura de inicio y final. Adicionalmente, en cada transecta, cada 10 metros se midió la altura media del dosel y se estimó el porcentaje de rocosidad (porcentaje con rocas). La regeneración arbórea se midió en 3 cuadrantes de 2x2m anidados en cada una de las transectas de adultos: al inicio (10 a 12m), en la zona media (50 a 52m) y hacia el final (90 a 92m). Se identificaron y midieron todos los juveniles arbóreos nativos y exóticos (altura ≥0,5 m y DAP <2,5 cm). En los mismos cuadrantes se realizó una evaluación fisonómica a través de la identificación de 9 categorías o estratos (suelo desnudo, mantillo, troncos caídos>10cm de diámetro, herbáceas, arbustos, regeneración arbórea, árboles de sotobosque, dosel y emergentes). De cada uno de estos estratos se estimó la cobertura (%) según las categorías de Braun-Blanquet (<1, 1-5, 6-25, 26-50, 51-75, 76-100). Asimismo, se determinó la altura de cada estrato vegetal. En cada cuadrante se midió la apertura del dosel con un densiómetro esférico. Para el relevamiento cualitativo de las especies leñosas se realizaron recorridas en los parches de bosque nativo, anotando todas las especies arbóreas y arbustivas observadas. Por último, las especies fueron clasificadas como zoocóricas o no según el tipo de fruto, observaciones de campo y referencias bibliográficas.

Resultados

Descripción de los componentes del paisaje relevados

Se presentan a continuación detalles de los sitios relevados y mapas simplificados de los mismos.

Los Arroyos y entorno

Se identificaron distintos componentes del paisaje (Figura 1-2). Se describen a continuación los ambientes nativos relevados mediante cámaras trampa.

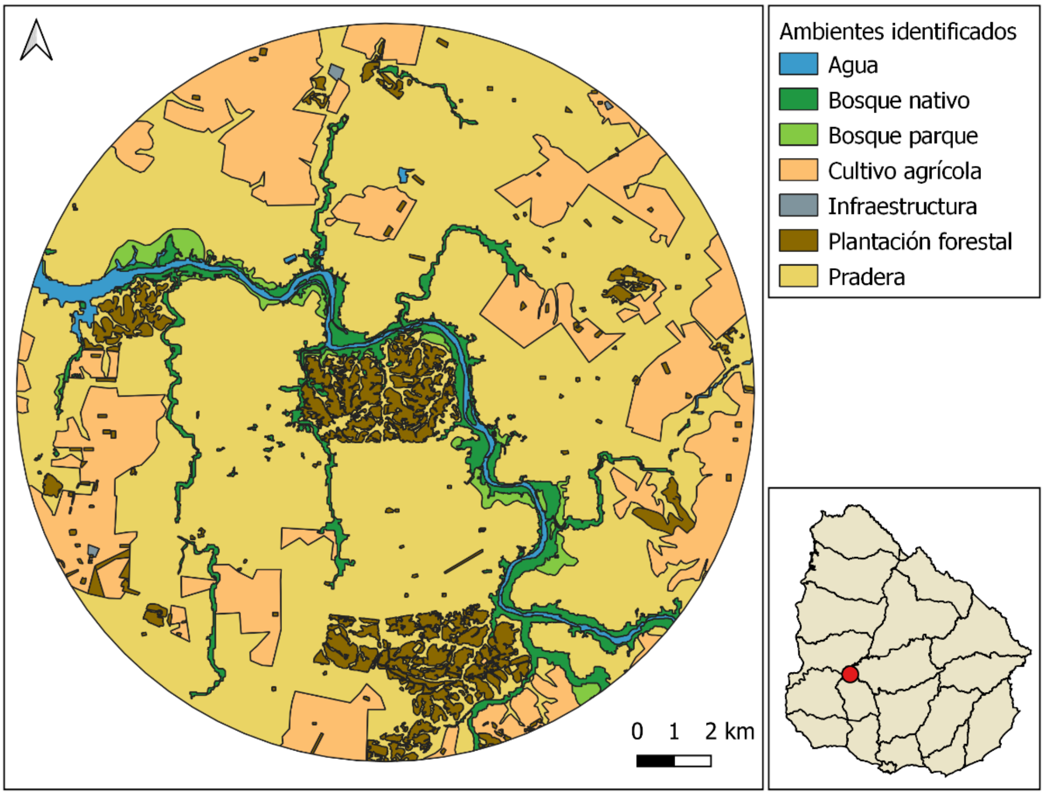

Figura 1-2 Componentes del paisaje identificados dentro del Establecimiento Los Arroyos y alrededores.

Se analizaron dos tipos de praderas (Figura 1-3). Las praderas rocosas presentan pendientes de suaves a moderadas. Fisonómicamente consiste en un pastizal, con arbustos y árboles dispersos asociados a afloramientos rocosos. En la vegetación se pueden distinguir los siguientes estratos:

- Herbáceo bajo: de hasta 0.1 m de altura, de cobertura bastante elevada. Está dominado por Gramíneas diversas.
- Herbáceo alto-subarbustivo: de 0.15-0.6 m de altura, de cobertura muy baja.
- Arbóreo-arbustivo: de 1-2.5 m de altura, de cobertura muy baja.

Las praderas medias, próximas a zonas de pradera rocosa y bordes de forestación, presentan pendiente suave a moderada, que normalmente terminan en praderas bajas o inundables asociadas a cañadas. Se trata de pastizales cortos y relativamente ralos, con algún árbol aislado, que forman parches de poca superficie, rodeados por vegetación herbácea más densa y alta. Se distinguen en general los siguientes estratos:

- Herbáceo bajo: de 0-0.1 m de altura, de cobertura media a baja. Está dominado por Gramíneas.
- Herbáceo alto-subarbustivo: de 0.15-0.5 m de altura, de cobertura muy baja.
- Arbustivo-arbóreo bajo: de 1-2 m de altura. Formado por escasos individuos aislados de *Acacia caven*.

Las praderas bajas son de pendiente suave, próximas a zonas inundables y pequeñas cañadas. El suelo (sin rocosidad en superficie) es relativamente húmedo, aunque no en forma permanente. Se trata de un pastizal denso, con escasos árboles dispersos. Se distinguen en general los siguientes estratos:

- Herbáceo bajo: de 0-0.1 m de altura, de cobertura casi total. Está dominado por Gramíneas.
- Herbáceo medio: de 0.1-0.4 m de altura, de cobertura baja a media.
- Herbáceo alto: de 0.4-1.5 m de altura, de cobertura muy baja.
- Arbustivo-arbóreo bajo: de 1.5-2.5 m de altura, de cobertura muy baja. Formado por ejemplares aislados de *Acacia caven*.

Figura 1-3 Praderas rocosa, media y baja. Los Arroyos

Se cubrieron tres tipos de bosque (Figura 1-4). En el bosque parque, el suelo es en general húmedo, sin casi rocosidad. En el momento del relevamiento (sin pastoreo reciente) el tapiz herbáceo es alto y denso con predominio de *Paspalum* sp. “Paja mansa”. La cobertura de mantillo es en general muy baja. El estrato herbáceo presenta una cobertura muy elevada, con una altura media de 0.65 m; está dominado por gramíneas. El estrato arbustivo tiene en promedio una cobertura baja, la altura media es de alrededor de 0.8 m; las especies más frecuentes son *Heimia salicifolia* y *Baccharis spicata.* La regeneración arbórea presenta en general cobertura muy baja y una altura media de alrededor de 1 m; las especies más abundantes son *Myrrhinium atropurpureum* y *Myrcianthes cisplatensis*. La cobertura media del dosel arbóreo es muy baja, con una altura variando de 2 a 4 m.

El relieve del bosque ribereño presenta los típicos albardones y canales; estos últimos son bastante profundos en algunos sectores. La cobertura de mantillo es en general bastante elevada. El estrato herbáceo presenta una cobertura generalmente baja, con una altura media de alrededor de 0.1 m; la composición es variable. El estrato arbustivo presenta una cobertura muy baja, una altura media de unos 0.25 m, y las especies principales son *Maytenus ilicifolia* y *Pavonia sepium*. La regeneración arbórea, de cobertura en general muy baja, tiene una altura media de unos 0.3 m, siendo las especies más abundantes *Eugenia uruguayensis* y *Allophylus edulis*. El estrato arbóreo de sotobosque es sumamente escaso, formado por individuos muy espaciados de 2 a 3.5 m. El dosel arbóreo presenta una cobertura muy elevada, con una altura de entre 6 y 9 m.

Dispersos en casi todo el establecimiento hay afloramientos rocosos a los que se encuentran asociados bosquetes y bosques formando parches generalmente de poca extensión, en laderas de pendiente general suave a moderada. Entre los parches de bosques se desarrollan pastizales sobre suelo relativamente húmedo. Los bosques son en general densos, con dosel bajo a medio. Pueden distinguirse tres estratos:

- Herbáceo: de 0-0.2 m de altura, de cobertura variable, en general relativamente alta. Está dominado por Gramíneas diversas.
- Arbustivo: de 0.5-1.5 m de altura, de cobertura muy baja. Formado principalmente por juveniles de *Myrcianthes cisplatensis.* Como especie arbustiva se encuentra *Cestrum parqui*.
- Arbóreo general: de 2-5 m de altura, de alta cobertura de copas. Las especies dominantes varían en distintos parches y sectores, entre ellas pueden mencionarse: *Eugenia uniflora, Myrcianthes cisplatensis, Sebastiania commersoniana, Zanthoxylum rhoifolium, Scutia buxifolia y Allophylus edulis.*

Figura 1-4 Bosques parque, ribereño y roquedal. Los Arroyos

El Matorral y entorno

Se identificaron distintos componentes del paisaje (Figura 1-5). Se describen a continuación los ambientes nativos relevados mediante cámaras trampa.

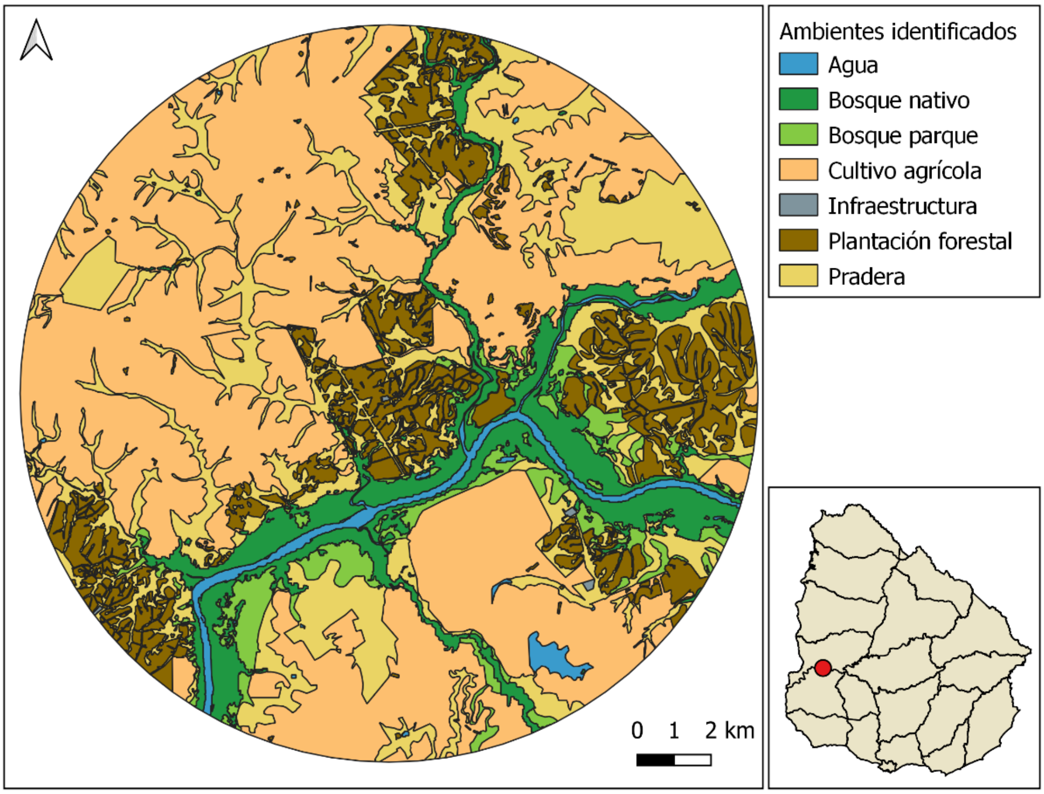

Figura 1-5 Componentes del paisaje identificados en el Establecimiento El Matorral y alrededores.

Las praderas bajas e inundables (Figura 1-6) tratan de pastizales densos de altura variable, asociados a parches de pajonales y juncales según el grado de humedad del suelo. En algunos sectores hay un estrato de árboles y arbustos dispersos formado principalmente por *Erythrina crista-galli, Salix humboldtiana, Sapium haematospermum* y *Cephalanthus glabratu*s.

Las praderas medias y rocosas (Figura 1-6) se ubican en lomadas de pendiente suave a moderada o algo fuerte, que terminan en escarpas rocosas y bordean algunos parches de forestación. La rocosidad es variable, en general de baja a media. La vegetación es principalmente herbácea, con presencia en algunos sectores de arbustos y árboles dispersos. En la vegetación se distinguen los siguientes estratos:

- Herbáceo bajo: de hasta 0.1 m de altura, de cobertura bastante alta. Formado principalmente por gramíneas. En este estrato, en los sitios de rocosidad elevada se destaca la presencia de Cactáceas.

- Herbáceo alto: de 0.1-0.4 m de altura, de cobertura también bastante alta. Formado principalmente por gramíneas. Entre las especies asociadas se destacan *Pterocaulon angustifolium* y *Psidium luridum*, típicas de este ambiente.
- Arbustivo: de 0.5-1 m de altura, de cobertura en general muy baja. Compuesto principalmente por *Acanthostyles buniifolius*.

Figura 1-6 Praderas bajas e inundables, medias y rocosas. El Matorral.

En el bosque ribereño (Figura 1-7), el relieve presenta los típicos albardones y canales en la planicie de inundación; la pendiente es moderada a fuerte y se observa una importante rocosidad en zonas. El suelo tiene en general elevada cobertura de mantillo. El estrato herbáceo presenta una cobertura en promedio relativamente alta, con una altura media de aproximadamente 0.15 m; las especies dominantes varían en distintos sectores, entre ellas se pueden mencionar *Blainvillea biaristata, Tradescantia fluminensis, Dichondra sp*., algunas Gramíneas y varias especies de helechos. El estrato arbustivo tiene en general una cobertura muy baja, y una altura media de alrededor de 0.5 m; las especies más frecuentes son *Maytenus ilicifolia, Pavonia sepium* y *Cestrum parquii*. La regeneración arbórea, de cobertura en general baja, tiene una altura media de aproximadamente 0.6 m; está dominada por Mirtáceas (*Eugenia uniflora, E. uruguayensis* y *Myrrhinium atropurpureum*), *Allophylus edulis* y *Sebastiania commersoniana*. El estrato arbóreo de sotobosque, con una altura de 2-3 m, es en general muy escaso, estando integrado principalmente por *Eugenia uruguayensis* al cual se asocia en algunos sectores *Sebastiania brasiliensis*. El dosel arbóreo tiene una cobertura en general alta, con una altura variando entre 4 y 8.5 m. En algunos sectores se observa un estrato arbóreo emergente de 9 a 12 m de altura.

Figura 1-7 Bosque ribereño. El Matorral.

En el bosque parque (Figura 1-8), el suelo, sin rocosidad, es en general húmedo a muy húmedo y anegable en varios sectores; hay algunas pequeñas cañadas en el entorno. Al momento del relevamiento el pastoreo había sido recientemente reintroducido. El estrato herbáceo tiene una cobertura prácticamente total y una altura promedio de 0.5 m; está dominado por diversas gramíneas, destacándose también la presencia de varias especies hidrófilas de las familias Cyperaceae y Juncaceae. El estrato arbustivo presenta una cobertura variable, con una altura promedio de alrededor de 0.6 m; las especies más frecuentes son *Heimia salicifolia* y *Baccharis spicata*. La regeneración arbórea tiene una cobertura muy baja, con una altura media (cuando presente) de 0.85 m; las especies más abundantes son *Sebastiania commersoniana* y *Blepharocalyx salicifolius*. El estrato arbóreo de sotobosque está prácticamente ausente. El dosel arbóreo, debido a la presencia de claros bastante amplios y la disposición dispersa de los árboles presenta una cobertura en promedio muy baja, con una altura media de 3.5 m.

Figura 1-8 Bosque parque. El Matorral.

Las Lilas y entorno

Se identificaron distintos componentes del paisaje (Figura 1-9). Se describen a continuación los ambientes nativos relevados mediante cámaras trampa.

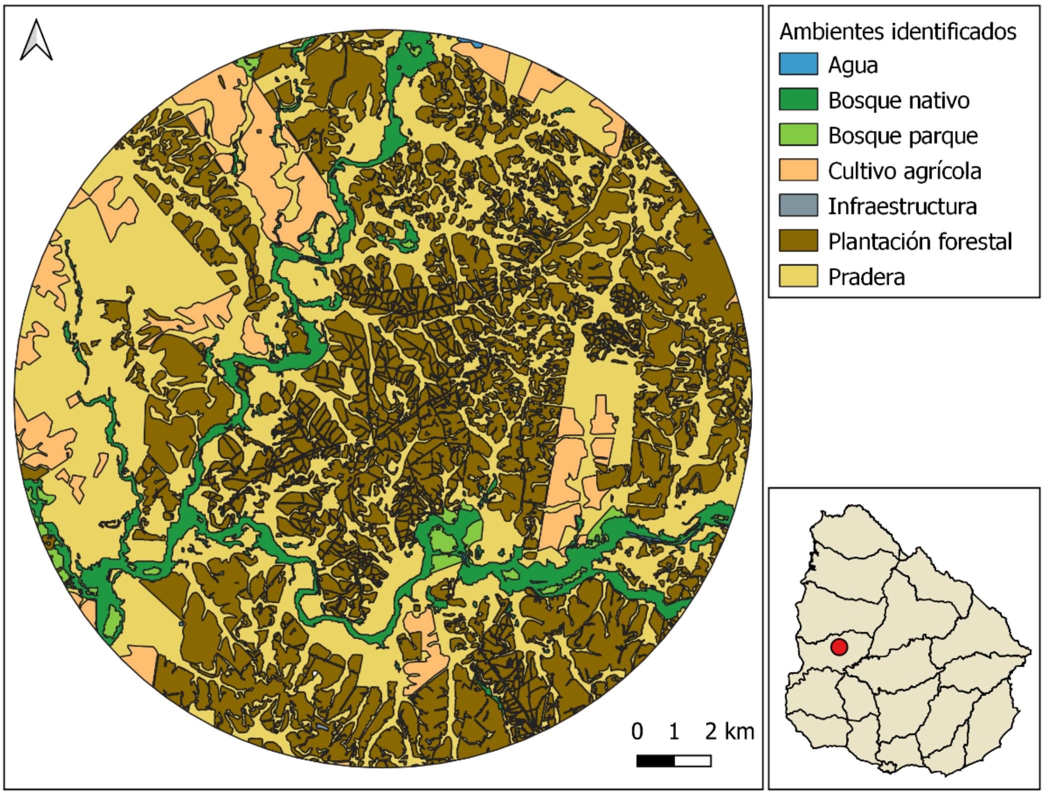

Figura 1-9 Componentes del paisaje identificados dentro del Establecimiento Las Lilas y alrededores.

Las praderas bajas e inundables (Figura 1-10) se desarrollan en las planicies de inundación de cañadas y arroyos, y a lo largo de las vertientes aledañas. En la vegetación se distinguen los siguientes estratos:

- Herbáceo bajo: de unos 0.1 m de altura, muy denso, está dominado por gramíneas.
- Herbáceo medio: de 0.1-0.5 m de altura, también muy denso. Presenta una alta riqueza de especies, incluyendo algunas leguminosas y diversas gramíneas destacándose los géneros *Poa* y *Chascolytrum*.
- Herbáceo alto: de 0.5-1.5 m de altura, de cobertura variable por sectores. Predominan las gramíneas *Paspalum quadrifarium* y *Sorghastrum pellitum*. En algunos sitios se asocian especies del género *Eryngium*.
- Arbustivo-arbóreo: de 1.5-2.5 m de altura, de cobertura muy baja. Está formado principalmente por *Vernonanthura montevidensis* y *Schinus longifolius*. En algunos

lugares próximos a cursos de agua se observan ejemplares de *Erythrina crista-galli* y pequeños matorrales de *Phyllanthus sellowianus*.

La pradera alta-rocosa (Figura 1-10) se ubica en lomadas de pendiente suave en la cima de los cerros. La rocosidad es variable, en general de baja a media. En la vegetación se distinguen los siguientes estratos:

- Herbáceo bajo: de hasta 0.1 m de altura, de cobertura en general alta. Formado principalmente por gramíneas. Se destaca la presencia de Cactáceas.
- Herbáceo alto: de 0.1-0.3 m de altura, de cobertura variable según el sitio. Dominado por gramíneas, asociándose a veces *Eryngium* sp.
- Arbustivo: 0.4-1.5 m de altura, de cobertura baja a casi nula. Integrado por *Acanthostyles buniifolius, Discaria americana* y *Colletia spinosissima*.

Figura 1-10 Praderas bajas e inundables y alta. Las Lilas.

En el bosque serrano (Figura 1-11) la pendiente es moderada a fuerte, disminuyendo hacia la pradera baja. La rocosidad es elevada en los sectores alto y medio de la ladera (formando en algunos sitios escarpas y pequeños paredones). Se observa la presencia de varias especies trepadoras y algunas epífitas. El suelo tiene en general elevada cobertura de mantillo. El estrato herbáceo presenta cobertura relativamente baja, con una altura media de 0.15-0.20 m; las especies principales son *Adiantum* sp., *Carex* sp. y *Bromus brchyanthera*; en este estrato se observó la presencia de la herbácea prioritaria *Mangonia tweediana*. En el estrato arbustivo, de cobertura muy baja y escasa altura (0.4 m), la especie más frecuente es *Maytenus ilicifolia*, hacia los bordes del bosque se destaca la presencia de *Colletia spinosissima*. La regeneración arbórea, de cobertura muy baja, tiene una altura media de 0.7 m, siendo *Myrcianthes cisplatensis* y *Myrrhinium atropurpureum* las especies más abundantes. El estrato arbóreo de sotobosque es muy escaso. El dosel arbóreo tiene una cobertura alta, con una altura variando entre 4 y 8m.

En los bosques ribereños (Figura 1-11) el relieve presenta los típicos albardones y canales. En algunos sitios hay pequeños afloramientos rocosos en el sector externo del bosque ribereño, que dan lugar a variaciones puntuales de la flora y fisonomía del bosque. Se trata en general de bosques densos. El área muestreada se encuentra en gran parte sin casi pastoreo. La cobertura de mantillo es en general elevada. El estrato herbáceo presenta cobertura baja, con una altura media de 0.10-0.15 m. El estrato arbustivo presenta en general cobertura baja, con una altura media de 0.5 m; está compuesto principalmente por *Maytenus ilicifolia* y *Pavonia sepium*. La regeneración arbórea, de cobertura variable, tiene una altura media de alrededor de 1 m, siendo las especies más abundantes *Allophylus edulis, Blepharocalyx salicifolius* y *Myrrhinium atropurpureum*. El estrato arbóreo de sotobosque es muy escaso. El dosel arbóreo presenta una cobertura muy elevada, con alturas de entre 5 y 8 m que disminuyen hacia el borde externo.

Figura 1-11 Bosques serrano y ribereño. Las Lilas.

Cueva del Tigre y entorno

Se identificaron distintos componentes del paisaje (Figura 1-12). Se describen a continuación los ambientes nativos relevados mediante cámaras trampa.

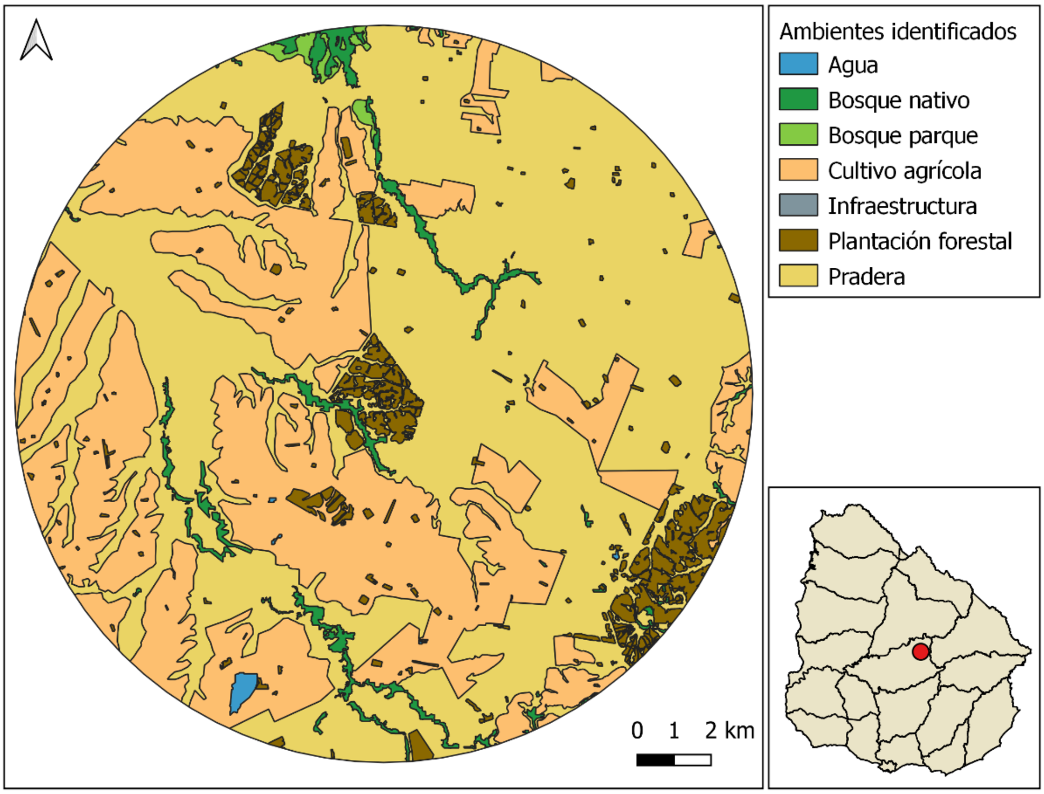

Figura 1-12 Componentes del paisaje identificados dentro del Establecimiento Cueva del Tigre y alrededores.

Las praderas bajas (Figura 1-13) se encuentran en las planicies de inundación de las cañadas, en las laderas bajas y a lo largo de las vertientes. Se trata de un pastizal alto y denso, en algunos sitios con características de pajonal, con pendiente suave a casi nula, asociado a vía de drenaje afluente a la cañada del Tigre. El suelo es húmedo a anegado, sin rocosidad en superficie. En la vegetación se pueden distinguir los siguientes estratos:

- Herbáceo bajo: de hasta 0.15 m de altura; de cobertura muy alta. Está dominado por Gramíneas diversas. El tapiz presenta una buena riqueza de especies.
- Herbáceo medio: de 0.2-0.6 m de altura, de cobertura bastante alta pero no total. Está también dominado por Gramíneas a los que se asocian ejemplares dispersos de *Adianthopsis chlorophylla* y *Erechtites hieracifolia*.
- Herbáceo alto-arbustivo: de 0.7-2 m de altura; de cobertura variable, en general relativamente alta. La especie dominante es *Erianthus* sp. “Paja estrelladora”, figurando como acompañante *Paspalum urvillei*. Como especie arbustiva aparece de manera escasa *Buddleja grandiflora*.

Figura 1-13 Pradera baja. Cueva del Tigre.

En el bosque de escarpa-serrano (Figura 1-14), existen escarpas relativamente grandes, que dan lugar a la formación paredones y pequeñas quebradas. La pendiente es variable, de suave a muy fuerte, siendo la rocosidad en general alta, y la humedad del suelo variable según la topografía. El suelo tiene en general elevada cobertura de mantillo. El estrato herbáceo presenta una cobertura en general alta, una altura media de 0.1 m, siendo las especies dominantes *Oplismenus hirtellus ssp. setarius*, *Panicum cf. ovuliferum* y *Carex sellowiana*; en los sitios más escarpados y húmedos se destaca la presencia de helechos. El estrato arbustivo, de cobertura media a relativamente alta y una altura promedio de 1 m, está dominado por *Daphnopsis racemosa, Pavonia sepium* y *Cestrum cf parquii*. La regeneración arbórea, de cobertura baja y una altura media de 1 m, presenta numerosas especies entre las que sobresale por su abundancia *Sebastiania commersoniana*. El estrato arbóreo de sotobosque presenta cobertura variable (de muy baja a relativamente alta), una altura media de unos 2.5 m, sin especies dominantes. El dosel arbóreo presenta alta cobertura de copas, con alturas variando entre 4.5 y 8 m (en general las mayores alturas se dan en quebradas húmedas). Ocasionalmente se observan ejemplares emergentes de entre 8 y 12 m, pertenecientes a *Ocotea acutifolia* y *Myrsine coriacea*.

En el bosque ribereño (Figura 1-14), la pendiente varía de casi nula a suave. El suelo, sin rocosidad en superficie, es relativamente húmedo, anegable en varios sitios y bastante arenoso en algunos sectores. La cobertura de mantillo es en general bastante elevada, aunque en algunos sectores hay cierta proporción de suelo desnudo. El estrato herbáceo presenta una cobertura alta y una altura media de 0.1 m; las especies dominantes son *Dichondra sp., Oplismenus hirtellus ssp. setarius* y *Carex sellowiana*; en los sectores más húmedos y de menor cobertura arbórea aparecen especies hidrófilas de los géneros *Polygonum* e *Hygrophylla*. El estrato arbustivo, de cobertura baja a media y una altura promedio de 0.6 m está dominado por *Daphnopsis racemosa, Pavonia sepium* y *Cestrum cf parquii*. La regeneración arbórea, de cobertura en promedio baja y una altura media de 0.85 m, está dominada por Mirtáceas (*Blepharocalyx salicifolius* y *Myrrhinium atropurpureum*), siguiéndoles en abundancia las especies del género *Sebastiania*. El estrato arbóreo de sotobosque presenta una cobertura variable, de nula a relativamente alta y una altura media de unos 3 m; la especie más frecuente es *Scutia buxifolia*. El dosel arbóreo presenta alta cobertura de copas, con alturas variando entre 4.5 y 9 m. Muy ocasionalmente se encuentran ejemplares emergentes de hasta 10 m.

Figura 1-14 Bosques de escarpa y ribereño. Cueva del Tigre.

Rincón del Río y entorno

Se identificaron distintos componentes del paisaje (Figura 1-15). Se describen a continuación los ambientes nativos relevados mediante cámaras trampa.

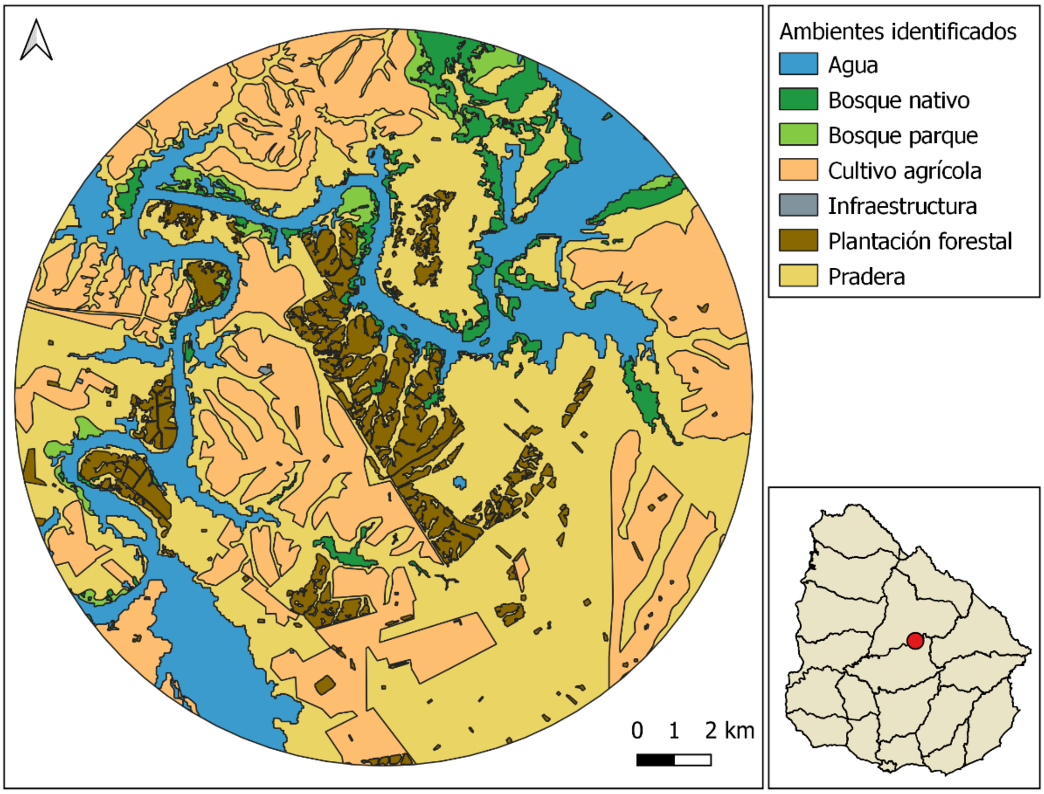

Figura 1-15 Componentes del paisaje identificados dentro del Establecimiento Rincón del Río y alrededores.

Se recorrieron tres tipos de praderas (Figura 1-16). Las praderas bajas se encuentran en las laderas asociadas a las vías de drenaje a lo largo de las vertientes y en las planicies y depresiones aledañas. En la vegetación se pueden distinguir los siguientes estratos:

- Herbáceo bajo: de 0.07 m de altura; de cobertura muy alta. Está dominado por Gramíneas diversas (por ej. *Axonopus* sp.).
- Herbáceo medio: de 0.5 m de altura; de cobertura media a baja. Está dominado por subarbustos (*Senecio grisebachii* y *Vernonia nudiflora* "Alecrín"). Como especies acompañantes se destacan *Baccharis trimera* y *Pterocaulon* sp.
- Herbáceo alto: de 0.8-1.8 m de altura; de cobertura muy baja. Está formado por individuos aislados o pequeños grupos de *Andropogon lateralis* ("Canutillo"), *Erechtites hieracifolia, Eryngium sp*. y *Cyperus* sp.

La pradera media es un pastizal denso, relativamente bajo. Se encuentra adyacente a bosque parque y cerca de bosquetes fluviales. En la vegetación se pueden distinguir los siguientes estratos:

- Herbáceo bajo: de 0.05-0.1 m de altura; de cobertura muy alta. Está dominado por Gramíneas.
- Herbáceo medio: de 0.1-0.5 m de altura; de cobertura variable por sectores, media a relativamente alta. Está dominado por Gramíneas.
- Herbáceo alto: de 0.5-1.2 m de altura; de cobertura muy baja. Está compuesto principalmente por *Andropogon lateralis*.
- Arbustivo-arbóreo bajo: de 1.5-2.5 m de altura; de cobertura muy baja. Formado principalmente por ejemplares aislados de *Acacia caven*. Los bosquetes están compuestos por especies leñosas de los bosques vecinos.

Las praderas inundables se presentan junto a las vías de drenaje a lo largo de las vertientes o en depresiones entre las laderas, estando generalmente asociados a las praderas bajas o a los bosques pantanosos. El suelo es muy húmedo a anegado. En la vegetación, con predominio de plantas emergentes, se pueden distinguir los siguientes estratos:

- Herbáceo bajo: de 0.1-0.2 m de altura, de cobertura muy elevada, y se encuentra anegado en la fecha de visita (noviembre de 2016). Está dominado por *Hydrocotyle* sp., Gramíneas diversas y *Myriophyllum aquaticum*.
- Herbáceo alto: de 0.3-1 m de altura, de cobertura variable siendo muy elevada donde domina *Typha* sp. "Totora" y media a baja donde domina *Eryngium cf. pandanifolium* "Caraguatá".
- Arbustivo: de 1.8-2.5 m de altura, de cobertura media a baja. Formado casi exclusivamente por *Eupatorium tremulum*. En los sectores sin *Typha* aparecen pequeños grupos de *Baccharis megapotamica*.
- Arbóreo bajo: de 3.5 m de altura, de cobertura muy baja. Formado por ejemplares aislados de *Erythrina crista-galli*.

Figura 1-16 Pradera baja, media e inundable. Rincón del Río.

También se recorrieron tres tipos de bosque (Figura 1-17). Los bosques pantanosos se desarrollan en forma de parches de tamaño variable en las depresiones entre laderas, asociados a vías de drenaje. Frecuentemente están rodeados por bañados y pajonales de ancho variable, a los que se asocian en algunos sitios arbustos o arbolitos como *Erythrina crista-galli, Eupatorium tremulum* y *Sesbania punicea*. La vegetación herbácea de estos bañados es generalmente densa, habiendo en algunos sitios parches de caraguatual (*Eryngium cf pandanifolium*) o pajonales de *Scirpus giganteus*. En el bosque, la altura, densidad y composición florística varían bastante entre parches y entre diferentes sectores de cada parche, dependiendo del grado de humedad del suelo y la distancia a los bordes. El suelo, de humedad variable, presenta en general elevada cobertura de mantillo, siendo en general muy humífero y aparentemente turboso en algunos sitios; es relativamente frecuente la presencia de musgos. El estrato herbáceo presenta cobertura variable, de media a muy alta, con una altura media de 0.5 m debido a la existencia de especies de alto porte como *Blechnum brasiliense*; otras especies frecuentes son *Carex sellowiana*, *Calyptocarpus biaristatus*, y helechos de los géneros *Thelypteris* y *Asplenium*; en los sectores de suelo más húmedo y hacia los bordes aparecen especies hidrófilas como *Adennostemma brasiliana, Boehmeria cylindrica, Hydrocotyle sp.* e *Hygrophylla sp*. El estrato arbustivo, de cobertura baja a media, tiene una altura promedio de 1 m; las especies más frecuentes son *Daphnopsis racemosa, Psychotria carthagenensis* y *Pavonia sepium*. La regeneración arbórea, de cobertura media y una altura promedio de 1.5 m, presenta una importante riqueza de especies; está dominada por Mirtáceas (particularmente *Eugenia uruguayensis*), siendo también comunes *Calliandra tweedii* y *Syagrus romazoffiana*. El estrato arbóreo de sotobosque tiene en promedio una cobertura baja, y una altura de 3.5 m; las especies más frecuentes son *Calliandra tweedii* y *Eugenia uruguayensis*. El dosel arbóreo presenta una cobertura en general muy elevada, con alturas variando entre 6 y 12 m.

En los bosques ribereños la pendiente varía desde casi nula en las planicies inundables, a suave o moderada en los sectores de laderas y hondonadas. No se observa prácticamente rocosidad en superficie. El bosque es inundable en los sectores de planicie y poco o no inundable en los sectores de ladera. Se trata en general de bosques densos y no muy altos, cuyas características florísticas y fisonómicas presentan cierta variación en los distintos sectores. El suelo tiene en general elevada cobertura de mantillo. El estrato herbáceo presenta una cobertura variable, en promedio baja y una altura media de aproximadamente 0.12 m; las especies dominantes varían en distintos sectores, entre ellas se pueden mencionar *Calyptocarpus biaristatus, Oplismenus hirtellus ssp. setarius* y *Acalypha multicaulis*. El estrato arbustivo tiene una cobertura muy variable, aunque en promedio relativamente baja y una altura media de 1.1 m; las especies más frecuentes son *Daphnopsis racemosa, Maytenus ilicifolia, Pavonia sepium* y *Cestrum cf. parquii*. La regeneración arbórea, de cobertura relativamente baja y una altura media de aproximadamente 1 m, está dominada por Mirtáceas (*Eugenia spp., Blepharocalyx, Myrcianthes cisplatensis, Myrrhinium*), siendo también frecuentes *Allophylus edulis* y *Sebastiania commersoniana*. El estrato arbóreo de sotobosque presenta cobertura variable (de muy baja a muy elevada), estando dominado por *Eugenia uniflora*. El dosel arbóreo presenta una cobertura en general elevada, con alturas variando entre 4 y 8 m. Ocasionalmente se observan ejemplares emergentes de hasta 10m.

Los bosques parque se desarrollan sobre lomadas o laderas adyacentes al bosque fluvial. La cobertura de mantillo es en general muy baja, siendo mayor bajo los bosquetes. El estrato herbáceo presenta una cobertura elevada, con una altura media de 0.16 m; está dominado por gramíneas. En algunos sectores se observa un estrato herbáceo alto, de de 0.1-0.6 m de altura; de cobertura variable; está también dominado por Gramíneas (se destacan grupos de *Aristida circinalis*) y por el subarbusto *Baccharis trimera*. El estrato arbustivo tiene en promedio una cobertura muy baja, con una altura media de 1 m; la especie más frecuente es *Daphnopsis racemosa*. El dosel arbóreo, de cobertura en general muy baja y alturas de entre 2-4 m está integrado casi totalmente por *Acacia caven* en los sectores más ralos, mientras que los bosquetes densos poseen composición variada, en general similar al bosque fluvial. En los bordes de bosquetes aparecen varias especies formando un estrato arbustivo, entre ellas *Schinus engleri, Daphnopsis racemosa, Eugenia uniflora*, etc. Si bien más escasa, la Cactácea *Cereus uruguayanus* es un elemento fisonómicamente característico de este bosque parque.

Figura 1-17 Bosques pantanoso, ribereño y parque. Rincón del Río.

Bequeló y entorno

Los principales ambientes presentes son: Bosque ribereño/bosque de escarpa, Bosque Parque-algarrobal, Praderas (Figura 1-18). El área tiene una superficie de aprox. 322 has. Está ubicada en la costa del Arroyo Bequeló (margen izquierda). El relieve presenta la planicie de inundación del arroyo Bequeló y sus principales tributarios (Arroyo Pelado) y escarpas rocosas ubicadas más o menos cerca de las vías de drenaje.

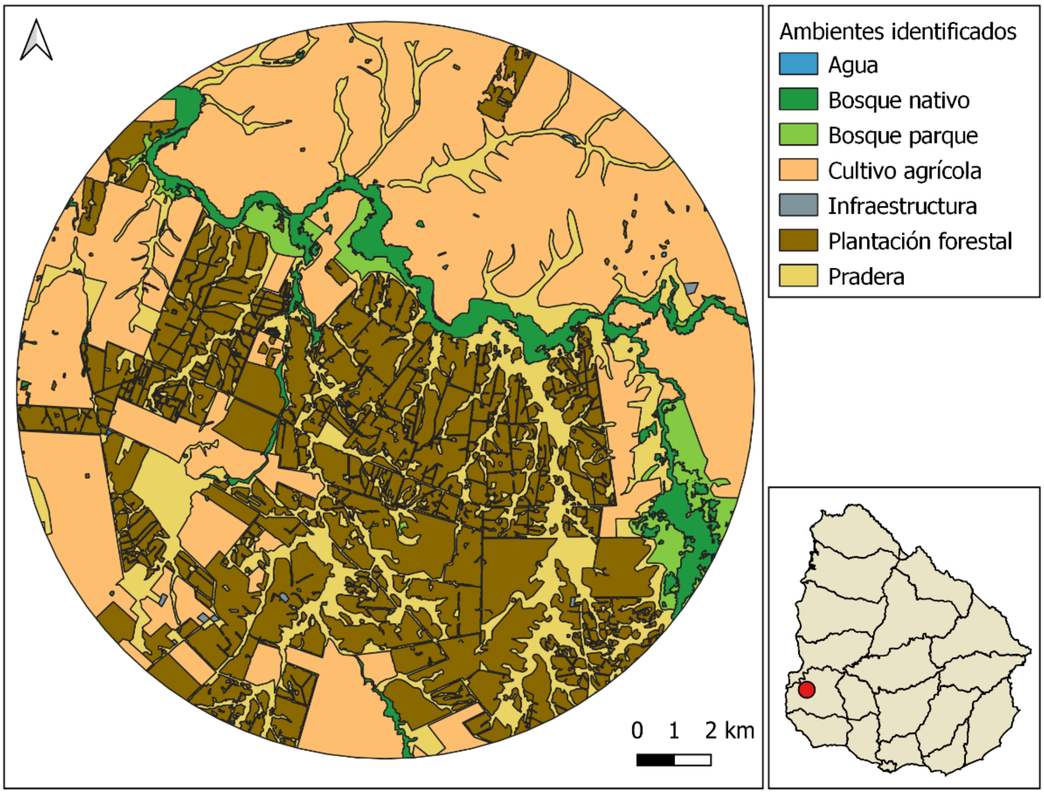

Figura 1-18 Componentes del paisaje identificados dentro del Establecimiento Bequeló y alrededores.

El bosque ribereño (Figura 1-19) se desarrolla de manera continua desde la orilla del arroyo hasta la cima de la escarpa dándose una transición más o menos gradual en el aspecto de la vegetación y la composición florística. El bosque es en general denso, alcanzando su máxima altura (8-10 m) en los sectores intermedios, disminuyendo hacia la escarpa.

En general se distinguen los siguientes estratos:

- Herbáceo: 20 cm de altura, de cobertura variable, generalmente media a alta. Las especies principales son: *Blainvillea biaristata*, *Tradescantia fluminensis*, *Asplenium ulbrichtii*, *Adiantum* sp.
- Arbustivo bajo: de aprox. 1 m de altura, baja cobertura. Las especies principales son: *Maytenus ilicifolia*, *Pavonia sepium* y juveniles de *Allophylus edulis*.

- Arbóreo: de aprox 8 m, con individuos emergentes de hasta 10 m. Las especies principales son: *Pouteria salicifolia*, *Ocotea acutifolia*.

El estado general de conservación en el sitio visitado es bueno, aunque existen sectores localizados con invasión de *Ligustrum lucidum* (adultos y juveniles), *Melia azedarach* y *Gleditsia triacanthos* (juveniles). Existen sectores de bosque secundario evidenciando tala, existe también evidencia de pisoteo y pastoreo leve.

Figura 1-19 Bosques ribereños. Bequeló.

En relación con el bosque parque y algarrobal (Figura 1-20), se encuentra en una planicie algo elevada respecto al arroyo y la cañada que lo rodean, estando sujeto a inundaciones ocasionales. La fisonomía es la típica de bosque parque, con árboles dispersos sobre un tapiz herbáceo continuo. La altura media del dosel es de 3 m. Dentro de esta matriz de parque se encuentran varios bosquetes, a menudo junto a *Trithrinax* y/o *Prosopis*, con predominio de *Celtis tala*, *Scutia buxifolia* y *Schinus longifolia*. Esta última especie forma bosque parque en planicie baja aledaña.

En general se distinguen los siguientes estratos:

- Herbáceo: 15-20 cm de altura, alta cobertura. Especies principales: diversas Gramíneas, *Desmanthus* spp., *Evolvulus* sp. Se destaca la presencia de algunas especies de blanqueal como *Gomphrena pulchella* y *Cienfuegosia sulphurea*.
- Arbustivo: 0.5-1.2 m de altura. De baja cobertura. Especies principales: *Geoffroea decorticans* y *Prosopis* sp. (juveniles).
- Arbóreo: 3 m de altura. Especie principal: *Prospis* sp. Se destaca la presencia de importante población de *Trithrinax campestris*.

El estado de conservación es en general bueno. El desarrollo del tapiz herbáceo y la presencia de juveniles de especies arbóreas indican que el pastoreo no es excesivo. Se registró la presencia de *Ligustrum lucidum* en muy baja abundancia, asociado a bosquecillos con *Trithrinax*.

Figura 1-20 Bosques parque. Bequeló.

Las praderas (Figura 1-21) se encuentran principalmente dentro de depresiones entre laderas, asociada a vías de drenaje tributarias del arroyo Bequeló. El suelo es relativamente húmedo y la pendiente escasa. La vegetación es principalmente herbácea y subarbustiva, con algunos arbustos dispersos. En general se distinguen los siguientes estratos:

- Herbáceo bajo: 5-10 cm de altura, alta cobertura. Especies principales: *Stenotaphrum secundatum*, *Phyla canescens*, *Dichondra* sp.
- Herbáceo alto/subarbustivo: 0.4-1 m de altura. La cobertura es variable, en general baja. Especies principales: *Piptochaetium stipoides*, *Paspalum* sp., *Centaurea* sp. (exótica) y *Heimia salicifolia*.
- Arbustivo: 1-1.5 m de altura. La cobertura es variable, baja a muy baja. Especies principales: *Baccharis punctulata* y *Heimia salicifolia*.

El estado de conservación es regular. Se observan alteraciones como el pisoteo de vías de drenaje por el ganado. También signos de degradación como la erosión activa de las orillas de vías de drenaje. En el tapiz herbáceo se encuentran algunas especies exóticas, aunque con poca abundancia: *Cynodon dactylon*, *Lolium* sp. Se destaca la presencia de abundantes juveniles de *Gleditsia triacanthos*.

Figura 1-21 Pastizales. Bequeló.

Santo Domingo y entorno

Se destacan dentro del presente establecimiento: el bosque ribereño correspondiente al arroyo Guaviyú y el bosque parque asociado, los palmares de Yatay típicos de la región y praderas inundables y bañados que integran el AAVC (Figura 1-22).

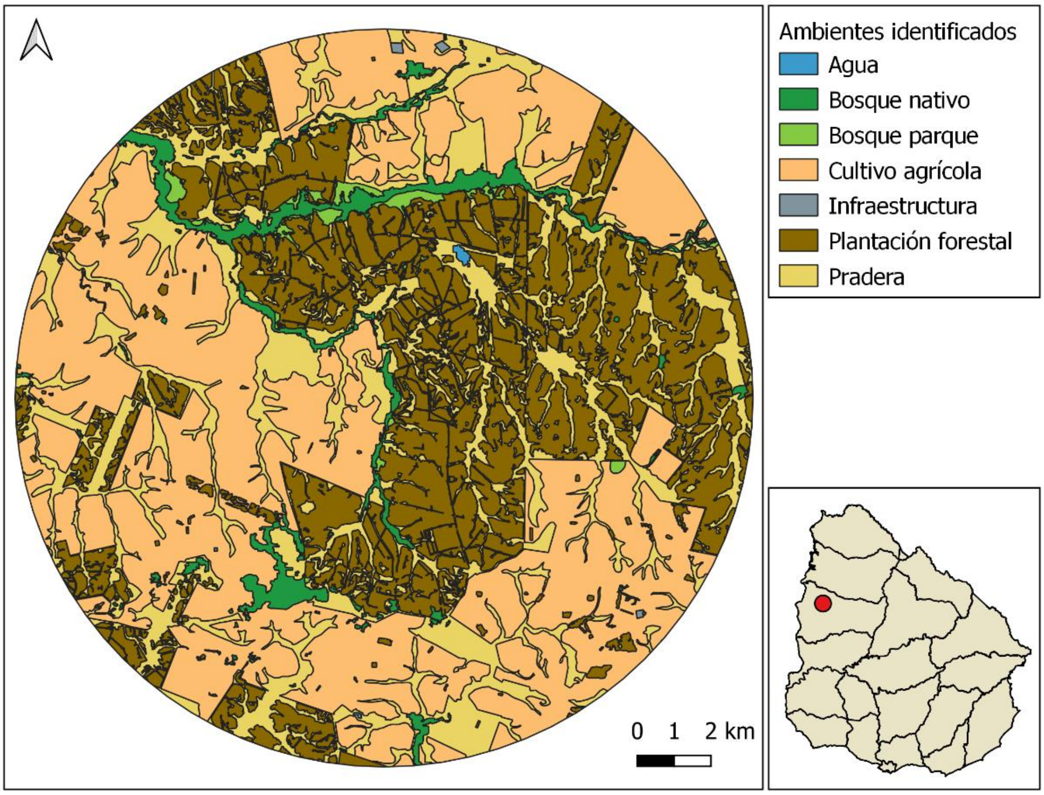

Figura 1-22 Componentes del paisaje identificados dentro del Establecimiento Santo Domingo y alrededores.

Los palmares de Yatay *Butia yatay* (Figura 1-23) configuran un tipo de ecosistema distintivo, constituyen un elemento relevante de la biodiversidad del cono sur de Sudamérica, especialmente para Argentina y Uruguay, donde persisten los mayores relictos. La extensión de presencia del ecosistema de palmar son 6.000 km2, distribuyéndose un 72% en Argentina, 27% en Uruguay y 1% en Brasil (Brazeiro et al., 2019). A los efectos de evitar los impactos del ganado en el palmar, en 1996 se estableció un área de exclusión en el establecimiento Santo Domingo, por lo que cuenta a la fecha con áreas excluidas y sin excluir de la ganadería presente. El estrato herbáceo presentó muy altas coberturas en los palmares, cercanas al 100%, tanto en áreas de exclusión al ganado como con acceso al pastoreo, sin embargo, en exclusión del ganado las herbáceas alcanzaron una mayor altura, prácticamente el doble al promedio registrado en pastoreo. La cobertura de arbustos en la exclusión antigua fue casi cinco veces mayor a la observada en pastoreo, y la altura promedio de este estrato fue más del doble. El estrato de palmeras regenerantes presentó valores bajos en todos los tratamientos, menores al 10%, y alturas que variaron entre 0.5 y 2.0 m. Sin embargo, la cobertura promedio de palmeras adultas en la exclusión antigua fue casi el doble a la observada en pastoreo. La altura máxima del estrato de palmeras adultas no varió entre tratamientos, y rondó los 9-10 m.

Figura 1-23 Palmar Yatay. Santo Domingo.

Las praderas bajas e inundables (Figura 1-24) tratan de pastizales densos de altura variable, asociados a parches de pajonales y juncales según el grado de humedad del suelo. En algunos sectores hay un estrato de árboles y arbustos dispersos formado principalmente por *Erythrina crista-galli, Salix humboldtiana, Sapium haematospermum* y *Cephalanthus glabratu*s. Presenta agua de manera permanente en la zona central del parche de mayor tamaño.

- Herbáceo bajo: de hasta 0.5 m de altura, de cobertura bastante alta. Formado principalmente por gramíneas.
- Herbáceo alto: de 1-1.5 m de altura, de cobertura también bastante alta. Formado principalmente por gramíneas. En algunos sitios se asocian especies del género *Eryngium*.
- Arbóreo: de 0.5-2 m de altura, de cobertura en general muy baja. Existen plantaciones álamos en el entorno.

Figura 1-24 Praderas bajas e inundables. Santo Domingo.

En el bosque ribereño (Figura 1-25), el relieve presenta los típicos albardones y canales en la planicie de inundación; la pendiente es moderada a fuerte y se observa una importante rocosidad en zonas. El suelo tiene en general elevada cobertura de mantillo. El estrato herbáceo presenta una cobertura relativamente alta, con una altura media de aproximadamente 0.20 m; las especies dominantes varían en distintos sectores, entre ellas se pueden mencionar *Blainvillea biaristata, Tradescantia fluminensis, Dichondra sp*., algunas Gramíneas y varias especies de helechos. El estrato arbustivo tiene en general una cobertura muy baja, y una altura media de alrededor de 0.7 m; las especies más frecuentes son *Maytenus ilicifolia, Pavonia sepium* y *Cestrum parquii*. La regeneración arbórea, de cobertura en general baja, tiene una altura media de aproximadamente 0.5 m; está dominada por Mirtáceas (*Eugenia uniflora, E. uruguayensis* y *Myrrhinium atropurpureum*), *Allophylus edulis* y *Sebastiania commersoniana*. El estrato arbóreo de sotobosque, con una altura de 3-4 m, es en general muy escaso, estando integrado principalmente por *Eugenia uruguayensis* al cual se asocia en algunos sectores *Sebastiania brasiliensis*. El dosel arbóreo tiene una cobertura en general alta, con una altura variando entre 6 y 9 m.

El bosque parque se da de manera muy transicional con el bosque ribereño, siendo particularmente arbolado (Figura 1-25). El suelo, sin rocosidad, es en general húmedo a muy húmedo y anegable en varios sectores; hay algunas pequeñas cañadas en el entorno. El estrato herbáceo tiene una cobertura muy alta y una altura promedio de 0.4 m; está dominado por diversas gramíneas, destacándose también la presencia de varias especies hidrófilas de las familias Cyperaceae y Juncaceae. El estrato arbustivo presenta una cobertura variable, con una altura promedio de alrededor de 0.8 m; las especies más frecuentes son *Heimia salicifolia* y *Baccharis spicata*. La regeneración arbórea tiene una cobertura muy baja, con una altura media (cuando presente) de 0.85 m; las especies más abundantes son *Sebastiania commersoniana* y *Blepharocalyx salicifolius*. El estrato arbóreo de sotobosque está prácticamente ausente. El dosel arbóreo, a la alta cobertura de árboles y la disposición por parche son tan dispersa de los árboles presenta una cobertura en promedio alta, con una altura media de 3 m.

Figura 1-25 Bosque ribereño y parque. Santo Domingo.

Dentro de la publicación correspondiente al ciclo forestal, se presentan más detalles estructurales de la vegetación, considerando incluso las etapas del ciclo forestal.

Flores (no forestado) y entorno

Se identificaron 2 componentes del paisaje (Figura 1-26): pastizales y bosque ribereño. Se detallan los mismos a continuación.

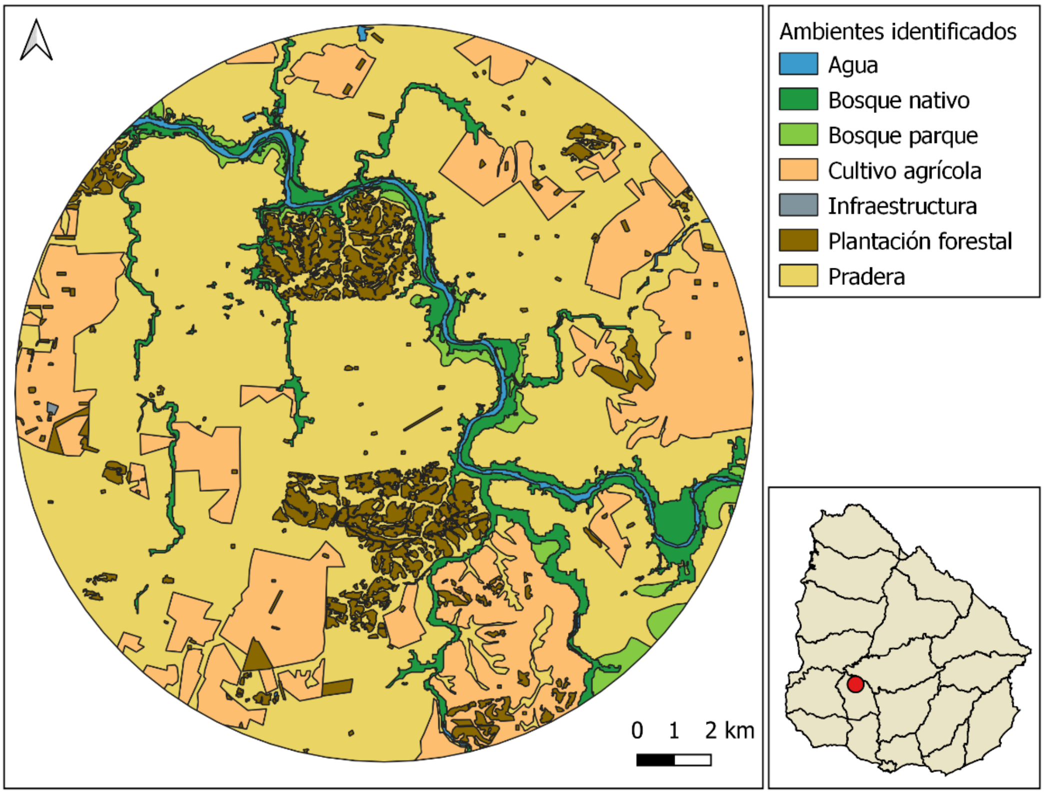

Figura 1-26 Componentes del paisaje identificados dentro del Establecimiento Flores y alrededores.

Se analizó un tipo de pradera (Figura 1-27). Las praderas monitoreadas, presentan pendiente suave a moderada, que normalmente terminan en praderas bajas o inundables asociadas a cañadas, con parches rocosos. Se trata de pastizales cortos y relativamente ralos (dada la presencia de ganado vacuno), con algún árbol aislado, que forman parches de poca superficie, rodeados por vegetación herbácea más densa y alta. Se distinguen en general los siguientes estratos:

- Herbáceo bajo: de 0-0.2 m de altura, de cobertura media a baja. Está dominado por Gramíneas. Aparecen paches rocosos.
- Herbáceo alto-subarbustivo: de 0.10-0.8 m de altura, de cobertura muy baja.
- Arbustivo-arbóreo bajo: de 1-2.5 m de altura. Formado por escasos individuos aislados de *Acacia caven*.

Figura 1-27 Praderas. Flores

El relieve del bosque ribereño (Figura 1-28) presenta los típicos albardones y canales; estos últimos son bastante profundos en algunos sectores. La cobertura de mantillo es en general bastante elevada. El estrato herbáceo presenta una cobertura generalmente baja, con una altura media de alrededor de 0.1 m; la composición es variable. El estrato arbustivo presenta una cobertura muy baja, una altura media de unos 0.25 m, y las especies principales son *Maytenus ilicifolia* y *Pavonia sepium*. La regeneración arbórea, de cobertura en general muy baja, tiene una altura media de unos 0.3 m, siendo las especies más abundantes *Eugenia uruguayensis* y *Allophylus edulis*. El estrato arbóreo de sotobosque es sumamente escaso, formado por individuos muy espaciados de 2 a 3.5 m de altura. El dosel arbóreo presenta una cobertura muy elevada, con una altura de entre 6 y 9 m.

Figura 1-28 Bosque ribereño. Flores

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