UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

ECOLOGÍA

EL EFECTO DEL DISTURBIO ANTROPOGÉNICO SOBRE LA INTEGRIDAD FUNCIONAL DE UN BOSQUE TEMPLADO DE MÉXICO: UNA EVALUACIÓN A TRAVÉS DE INDICADORES

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

M. en C. LETICIA BONILLA VALENCIA

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CIUDAD UNIVERSITARIA, CD. MX., NOVIEMBRE, 2021

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CIUDAD UNIVERSITARIA, CD. MX., 2021

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión virtual del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 9 de agosto del 2021 se aprobó el siguiente jurado para el examen de grado de **DOCTOR(A) EN CIENCIAS** de la estudiante **BONILLA VALENCIA LETICIA** con número de cuenta **307034492** con la tesis titulada "**EL EFECTO DEL DISTURBIO ANTROPOGÉNICO SOBRE LA INTEGRIDAD FUNCIONAL DE UN BOSQUE TEMPLADO DE MÉXICO: UNA EVALUACIÓN A TRAVÉS DE INDICADORES**", realizada bajo la dirección de la **DRA. SILVIA CASTILLO ARGÜERO,** quedando integrado de la siguiente manera:

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Secretario:	DR. ROBERTO ANTONIO LINDIG CISNEROS

Sin otro particular, me es grato enviarle un cordial saludo.

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"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 27 de octubre de 2021

COORDINADOR DEL PROGRAMA

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A mis padres Dolores y Crescencio, y a mi abuela Rosa

Índice

Resumen

Aunque actualmente a nivel global el incremento de las actividades humanas y la entrada de especies de malezas representan una de las principales amenazas para la integridad funcional de las comunidades, son pocos los estudios que han evaluado sus impactos en esta escala. Uno de los problemas ha sido la ausencia de indicadores funcionales que incluyan la complejidad del efecto antropogénico sobre la modificación de la composición de especies y sus consecuencias sobre los procesos ecológicos relacionados con la integridad funcional de las comunidades (e.g., procesos de regeneración natural). Por lo cual, en esta investigación se propone la aplicación de las métricas de diversidad funcional como indicadores ecológicos que permiten identificar y aislar características claves de las especies que contribuyen con procesos ecológicos a escala de comunidad.

Esta tesis muestra la aplicación de la diversidad funcional como indicador ecológico, desde una perspectiva teórica, metodológica y aplicada. Para lograr esto, primero se presenta un artículo de revisión que demuestra con evidencia empírica que la diversidad funcional es un indicador ecológico de respuesta funcional de las especies a factores de perturbación antropogénica. Consecutivamente, se presenta un artículo de investigación, en el cual, se desarrolla una nueva propuesta metodológica nombrada *"Inferencia Lógica por Abducción"*; que permite la construcción de indicadores funcionales a través de ecuaciones estructurales (SEM, por sus siglas en inglés Structural Equation Modeling). Este método permite la selección de los indicadores funcionales más plausibles para explicar la cadena causal del efecto de las actividades antropogénicas sobre la respuesta funcional de las especies y sus efectos sobre los cambios de composición. A partir de este método fue posible demostrar que el incremento de las actividades antropogénicas tiene un efecto diferente sobre la respuesta funcional de las especies características (i.e., especies nativas comunes establecidas en zonas conservadas) y malezas (i.e., especies nativas o introducidas establecidas bajo condiciones de perturbación antropogénica).

Finalmente se presenta un segundo artículo de investigación en el cual se aplica el método de *"Inferencia Lógica por Abducción"* con el propósito de evaluar el efecto antropogénico sobre la integridad funcional del bosque de *Abies religiosa* de la cuenca del río Magdalena, Ciudad de México. Un bosque que presenta constantes actividades de ganadería y de deforestación que han favorecido el incremento continuo de especies de malezas. En este bosque se determinaron indicadores de disturbios antropogénico, ambiéntale e indicadores de vulnerabilidad de ensamblaje (riqueza de especies, composición y diversidad funcional) en los componentes de la vegetación relacionados con los procesos de regeneración natural (banco de semillas, lluvia de semillas y vegetación).

La integración de estos indicadores a través de SEM y los análisis RLQ demostró que la ganadería y el deterioro del hábitat promueven un efecto de retroalimentación positiva que favorece continuamente la entrada de especies de malezas con una alta diversidad funcional en el banco y la lluvia de semillas. Mientras que, en la vegetación, los disturbios antropogénicos actúan como nuevos filtros de selección que favorecen el establecimiento de malezas con atributos y tolerancias similares asociados a una historia de vida ruderal (i.e., herbáceas con semillas de masa pequeña) y que presentan una estrategia adquisitiva de recursos (i.e., especies con valores altos de área foliar especifica). En esta situación, se predice que la comunidad tiene una baja probabilidad de recuperar su ensamblaje histórico. Por lo tanto, probablemente el bosque de *A. religiosa* se conducirá hacia un estado alternativo estable funcionalmente homogéneo y dominado por especies de malezas; el cual necesitara de actividades de restauración para recuperar su función original. Se concluye que el desarrollo de indicadores funcionales a través del método de *Inferencia Lógica por Abducción"* representa una importante herramienta en la teoría de indicadores que facilita la predicción del impacto antropogénico en la integridad funcional de las comunidades.

Palabras clave: diversidad funcional, atributos funcionales, modelos de ecuaciones estructurales, especies de malezas, especies características.

Abstract

Although currently and globally, the increase of human activities and the entry of weed species represent one of the main threats to the functional integrity of communities, few studies have evaluated their impacts at this scale. One of the problems has been the absence of functional indicators that include the complexity of the anthropogenic effect on the modification of the species composition and its consequences on the ecological processes related to the functional integrity of the communities (e.g., natural regeneration processes). Therefore, this research proposes the application of functional diversity metrics as ecological indicators that allow identifying and isolating critical characteristics of species that contribute to ecological processes at the community level.

This thesis shows the application of functional diversity as an ecological indicator from a theoretical, methodological, and applied perspective. To achieve this, we first present a review article, which demonstrates with empirical evidence that functional diversity is an ecological indicator of functional response of species to anthropogenic disturbance factors. Consecutively, a new methodological proposal named "*Logical Inference by Abduction*" is presented in a research article; that allows the construction of functional indicators through structural equations (SEM; Structural Equation Modeling). This method allows the selection of the most plausible functional indicators to explain the causal chain of the effect of anthropogenic activities on the functional response of the species and its effects on changes in species composition. From this method, it was possible to demonstrate that the increase in anthropogenic activities has a different impact on the functional response of characteristic species (i.e., native species common in conserved areas) and weeds (i.e., native or introduced species common in anthropogenically disturbed areas).

Finally, a second research article is presented in which the method of *"Logical Inference by Abduction"* is applied to evaluate the anthropogenic effect on the functional integrity of the *Abies religiosa* forest of the Magdalena River basin, Mexico City. A forest under constant livestock and deforestation activities that have favored the continuous increase of weed species. In this forest, anthropogenic and environmental disturbances indicators and assembly vulnerability indicators

(species richness, composition, and functional diversity) in the vegetation components associated with natural regeneration processes (seed bank, seed rain, and vegetation) were determined.

The integration of these indicators through SEM and RLQ analyses demonstrated that livestock and habitat deterioration promote a positive feedback effect that continually favor the entry of weed species with high functional diversity in the seed bank and seed rain. While, in vegetation, anthropogenic disturbances act as new selection filters that favor the establishment of weeds with similar attributes and tolerances associated with a ruderal life history (i.e., herbaceous with low seed mass) and that present an acquisitive resources strategy (i.e., species with a high specific leaf area). Under this situation, the community is predicted to have a low probability of recovering its historical assemblage. Therefore, it is likely that the *A. religious* forest will move towards a functionally homogeneous stable alternative state dominated by weed species; and will require restoration activities in order to recover its original function. It is concluded that the development of functional indicators through the method of *"Logical Inference by Abduction"* represents an important tool in indicator theory that facilitates the prediction of the anthropogenic impact on the functional integrity of communities.

Keywords: functional diversity, functional traits, structural equation models, weed species, characteristic species.

CAPÍTULO 1

INTRODUCCIÓN GENERAL

CAPÍTULO 1

INTRODUCCIÓN

EL EFECTO ANTROPOGÉNICO SOBRE LA INTEGRIDAD FUNCIONAL DE LAS COMUNIDADES

El acelerado crecimiento de las actividades humanas, como la deforestación y la ganadería ponen en riesgo el mantenimiento de los procesos de las comunidades (e.g., la polinización, y la dispersión); los cuales brindan diferentes bienes servicios para el desarrollo humano (Mayfield *et al.,* 2010; Mouillot *et al.,* 2013). Sin embargo, a pesar de esta situación, actualmente son pocos los estudios que han logrado determinar los efectos de los disturbios antropogénicos sobre la integridad funcional de las comunidades (Zakharova *et al.,* 2019; Glatthorn *et al.,* 2021). La integridad funcional hace referencia a la capacidad de una comunidad para mantener a través del tiempo un sistema biológico equilibrado e integrado por la gama completa de procesos de la vegetación nativa característica (Woodwell, 2002; Song *et al.,* 2014; Glatthorn *et al.,* 2021). Por lo que su estudio, frecuentemente excede los alcances metodológicos y limita con ello el desarrollo de estrategias de manejo y conservación en la mayoría de los ecosistemas (Díaz y Cabido 2001; Song *et al.,* 2014). En el presente se requieren de nuevas aproximaciones y estrategias metodológicas para reducir la complejidad inherente de los procesos y poder predecir los efectos de las actividades antropogénicas a nivel funcional.

Actualmente, la implementación de los indicadores ecológicos ha demostrado ser una estrategia eficaz para evaluar el impacto antropogénico sobre las comunidades de plantas en varios ecosistemas (OECD 1994; Niemeijer y Groot, 2008; Santibáñez-Andrade *et al.,* 2015). Los indicadores ecológicos son parámetros cuantitativos y cualitativos que resumen información compleja acerca del estado de conservación o degradación (Niemeijer y Groot 2008; Müller *et al.*, 2012). El objetivo principal de un indicador es reducir el exceso de información, aislando los aspectos clave de las condiciones ambientales para ayudar a determinar acciones apropiadas de manejo y conservación (Niemeijer y Groot, 2008). Sin embargo, a pesar de sus características y su creciente interés, la aplicación de los indicadores ecológicos en la evaluación del estado

funcional a nivel de comunidad ha encontrado diferentes limitaciones como problemas con (1) la recopilación de una extensa cantidad de información para caracterizar un proceso particular (Rempel *et al.,* 2016; Mora *et al.,* 2019) y (2) el uso de métricas de diversidad taxonómica, como indicadores ecológicos de conservación (Mayfield *et al.,* 2010; Mouillot *et al.,* 2013). Tal situación puede obstaculizar la evaluación del impacto antropogénico, dado que, el efecto de los disturbios antropogénicos es diferente entre unidades taxonómicas (Mayfield *et al.,* 2010) y la contribución de las especies también es diferente sobre los procesos ecológicos (Song *et al.,* 2014).

Conocer el papel funcional de las especies sobre el mantenimiento de los procesos ecológicos y funciones es uno de los principales retos en el desarrollo de los indicadores ecológicos (Cadotte *et al.,* 2011; Song *et al.,* 2014; Hines, 2019). El termino "*función" (es)* hace referencia al vinculo que existe entre las características de las comunidades, como los atributos de las especies con diferentes procesos (e. i., interacciones y conexiones entre sistemas vivos y no vivos, incluidos los movimientos de materia, energía, y la dinámica de las comunidades (Noss 1990; Giller *et al.,* 2004; Song *et al.,* 2014; Glatthorn *et al.,* 2021). Para Glatthorn *et al.* (2021) es posible distinguir tres funciones principales; (1) funciones mecánicas; característica que describen una tasa de cambio a nivel del ecosistema durante un período de tiempo, por ejemplo, el almacenamiento de biomasa en pie relacionado con el proceso de productividad (Mason *et al.,* 2016; Smart *et al.,* 2017; Li *et al.,* 2021ab; Glatthorn *et al.,* 2021). (2) Funciones de abastecimiento: característica de los ecosistemas que brindan bienes y servicios para el desarrollo humano, por ejemplo, la captura de carbono relacionado con el proceso de productividad (Díaz *et al.,* 2007; Glatthorn *et al.,* 2021). (3) Funciones de integridad ecológica: características de los ecosistemas y las comunidades relacionadas con el mantenimiento de los procesos ecológicos a través del tiempo y los cuales contribuyen con el mantenimiento de otras funciones; por ejemplo, atributos de las comunidades que favorecen los procesos de regeneración natural (Woodwell, 2002; de Bello *et al.,* 2010; Glatthorn *et al.,* 2021).

Actualmente la diversidad de atributos funcionales esta emergiendo como una vía accesible para conocer la contribución de las especies sobre diferentes funciones y procesos ecológicos que se relacionan con la integridad funcional en las comunidades (Hines, 2019). La

diversidad funcional incluye el conjunto de atributos morfológicos, fisiológicos y fenológicos de las especies que determina su establecimiento, crecimiento supervivencia y reproducción y los cuales influyen directamente en los procesos ecológicos (Tilman *et al.,* 1997; Díaz y Cabido, 2001; Poorter *et al.,* 2008; Song *et al.,* 2014). Por ejemplo, se ha demostrado que bajo condiciones de perturbación antropogénica la disminución de la diversidad de atributos florales se encuentra directamente relacionada con el decremento de las interacciones de polinización de una comunidad (Girão *et al.,* 2007). En consecuencia, la diversidad funcional parece ser una estrategia viable para desarrollar indicadores ecológicos que evalúen el efecto antropogénico sobre la respuesta funcional de las especies y predecir los cambios en la integridad funcional.

LA APLICACIÓN DEL ENFOQUE DE LA DIVERSIDAD FUNCIONAL COMO INDICADOR; RETOS Y SOLUCIONES ANTE UN ESCENARIO DE DISTURBIO ANTROPOGÉNICO

El desarrollo de los indicadores ecológicos basados en la diversidad funcional plantea nuevos retos, que implican desde la construcción de un marco conceptual hasta el desarrollo de nuevas estrategias metodológicas (Mason y Bello, 2013; Zakharova *et al.,* 2019). Actualmente, la mayoría de los indicadores ecológicos disponibles se basan en un marco conceptual de cadena causal, en los cuales las actividades antropogénicas se consideran fuerzas impulsoras que ejercen presión sobre los componentes de composición, función y estructura en las comunidades (i.e., Presión-Estado-Respuesta; Fuerza Conductora-Presión-Estado-Impacto-Respuesta) (Dale y Beyeler, 2001; Niemeijer y Groot, 2008; Li *et al.,* 2021b). Por ejemplo, bajo este esquema frecuentemente se han promovido la aplicación de la abundancia de las especies de malezas como un indicador directo de la magnitud del impacto antropogénico (Sheley *et al.,* 2010; Helm *et al.,* 2015; Santibáñez-Andrade *et al.,* 2015). Las malezas se definen como especies nativas y/o introducidas altamente competitivas, cuyo establecimiento, crecimiento y reproducción es favorecido en sitios con alta perturbación antropogénica (Espinosa and Sarukhán 1997; Richardson *et al.,* 2000; Calderón de Rzedowski and Rzedowski 2001; Drenovsky *et al.,* 2012ab; Vibrans 2015). Si bien, los indicadores basados en la abundancia de malezas han ayudado a desarrollar diferentes estrategias de manejo, investigaciones recientes demuestran que el éxito de las especies de malezas se debe a la presencia de atributos funcionales y tolerancias similares a la perturbación antropogénica (Mayfield *et al.,* 2010). Por lo tanto, es necesario desarrollar nuevos

métodos que consideren que las actividades antropogénicas actúan primero sobre la repuesta funcional de las especies y posteriormente sobre los cambios en la composición.

Los enfoques de cadena causal probablemente también limitan la interpretación de los indicadores. Por ejemplo, algunos estudios que utilizan las métricas de diversidad funcional como indicador ecológico, frecuentemente interpretan los valores altos de diversidad funcional como un indicador de un buen estado de integridad ecológica (Díaz *et al*., 2007; Duflot *et al*., 2014; Capmourteres and Anand, 2016). Sin embargo, es necesario considerar que, bajo condiciones de perturbación antropogénica, la colonización y el establecimiento de especies de malezas puede propiciar la entrada de nuevos atributos funcionales para la comunidad y promover incrementos de la diversidad funcional (Mayfield *et al.,* 2010; Mouillot *et al.,* 2013). Por lo tanto, para poder predecir el efecto antropogénico sobre el estado funcional de las comunidades son necesarias nuevas estrategias metodológicas que permitan diferenciar la contribución de las especies en los procesos ecológicos.

LA REGENERACIÓN NATURAL: UN PROCESO CLAVE PARA PREDECIR EL IMPACTO ANTROPOGÉNICO SOBRE LA INTEGRIDAD FUNCIONAL

La regeneración natural se define como el reemplazamiento de los individuos maduros de una comunidad por individuos de la siguiente generación, e integra los procesos de fenología reproductiva, la dispersión de semillas, la formación del banco de semillas, la germinación y el establecimiento de especies (Ma *et al.,* 2010; Fischer *et al.,* 2016; Larson y Funk, 2016; Ma *et al.,* 2019). La teoría del ensamblaje predice que después de un evento de perturbación los procesos de regeneración natural promueven la recuperación del ensamblaje (Auffret y Cousins, 2011; Larson y Funk, 2016). Esto a través del reclutamiento de nuevos individuos de especies características, las cuales se definen como especies nativas típicas de áreas conservadas a partir de la lluvia de semillas y el banco de semillas (Pakeman *et al.,* 2013; Larson y Funk, 2016). Estas especies presentan una gran variedad de atributos funcionales con adaptaciones a los regímenes ambientales y de perturbación natural que favorece su reclutamiento y el mantenimiento continuo de los procesos originales a través del tiempo (Gioria *et al.,* 2012; Gioria y Pyšek, 2015; Johnston

et al., 2016). Sin embargo, a diferencia de los disturbios naturales, las perturbaciones antropogénicas modifican drásticamente la dinámica de la regeneración natural, debido a que irrumpen la disponibilidad y movilidad de los propágulos presentes y modifican las condiciones requeridas para la germinación y establecimiento de las especies características (Ghazoul *et al.,* 2015; Fischer *et al.,* 2016; Dey *et al.,* 2018). En esta situación, se limitan la regeneración natural de diferentes especies características y se favorece la dispersión y/o establecimiento de especies de malezas, las cuales presentan atributos funcionales que modifican y alteran drásticamente los procesos originales de las comunidades (Mayfield *et al.,* 2010; Drenovsky *et al.,* 2012a; Martínez-Orea *et al.,* 2014).

El efecto de los disturbios antropogénicos sobre las condiciones ambientales frecuentemente intensifica los filtros ambientales preexistentes y actúa como un nuevo filtro de selección, que promueve un efecto de convergencia funcional sobre el ensamblaje de las especies (Mayfield *et al.,* 2010; Ulrich *et al.,* 2017). En áreas altamente perturbadas donde existe una alta colonización y establecimiento de malezas, la intensificación de los filtros ambientales regularmente favorece la presencia de especies de malezas que presentan un conjunto de atributos y tolerancia similares a los regímenes recurrentes de perturbación (Baker, 1974: Richardson *et al.,* 2000; Mayfield *et al.,* 2010; Zimdahl, 2013). Esto probablemente ocurre porque muchas especies de malezas comparten atributos de regeneración similares; como semillas pequeñas que son fácilmente dispersadas por el viento a largas distancias y mecanismos de latencia que favorece su permanencia por largos periodos de tiempo en el banco de semillas (Martínez-Orea *et al.,* 2014; Gioria y Pyšek, 2015; Funk *et al.,* 2017).

Si bien muchos de los estudios realizados en ambientes altamente perturbados, han reportado que las especies de malezas promueven un efecto de homogeneidad funcional (convergencia funcional), estas especies también puede favorecer la entrada de nuevos atributos funcionales en las comunidades (Flynn *et al.,* 2009; Martínez-Orea *et al.,* 2014; Gioria y Pyšek, 2015). Las perturbaciones antropogénicas pueden propiciar cambios ambientales que promueven la eliminación de filtros ambientales y con ello propician nuevos nichos disponibles que favorecen la entrada de especies de malezas con una alta diversidad funcional (Mayfield *et al.,* 2010). Bajo esta situación, se promueve un efecto de divergencia funcional; que favorece

gradualmente la presencia de malezas introducidas con atributos funcionales diferentes a los atributos presentes en las especies características (Mayfield *et al.,* 2010; Fried *et al.,* 2019). Por ejemplo, las especies de malezas introducidas frecuentemente presentan una alta diversidad de atributos florales y patrones fenológicos asincrónicos que favorecen una alta adquisición de recursos abióticos y abióticos en temporadas del año diferentes al de las especies características (Girão *et al.,* 2007; Bonilla-Valencia *et al.,* 2017). Estos cambios a largo plazo pueden irrumpir muchas de las interacciones de las especies características y generar cambios drásticos en los procesos de polinización y dispersión (Wolkovich y Cleland, 2010; Morellato *et al.,* 2016; Bonilla-Valencia *et al.,* 2017; Fried *et al.,* 2019). Por lo tanto, el estudio de las composición y de los atributos de las especies presentes en las fuentes de regeneración natural (i.e,, el banco y la lluvia de semillas) podrían ser considerados indicadores ecológicos clave para predecir el ensamblaje de las especies que se desarrollara en un futuro en las comunidades y a través de los cuales es posible evaluar la integridad funcional (Pakeman *et al.,* 2013; Larson y Funk, 2016; Capmourteres and Anand, 2016; Zakharova *et al.,* 2019; Glatthorn *et al.,* 2021).

Aunque diferentes estudios ecológicos pioneros han agrupado a las especies en función de sus atributos de regeneración natural (e.g., estudios de germinación y banco de semillas, Thompson, 2000; Grime *et al.,* 2006), estos atributos rara vez se han incorporado en las métricas de diversidad funcional (Larson y Funk, 2016). Probablemente, esto se debe a las diferencias conceptuales que tienen ambos enfoques (Clark *et al.,* 1999; Grace, 1991; Grime *et al.,* 2006; Dey *et al.,* 2018; Craine, 2005; Funk *et al.,* 2017). Históricamente los atributos asociados con los procesos de regeneración natural se han abordado desde el concepto de nicho de regeneración natural (Grubb, 1977; Lavorel y Chesson, 1995), el cual explica la coexistencia de especies con atributos de historia de vida similares (Craine, 2005; Funk *et al.,* 2017). Por el contrario, las métricas de diversidad funcional recientemente desarrolladas subyacen en la hipótesis del "efecto de complementariedad de nicho" propuesta por Tilman *et al.,* (1997), que se enfoca en la disimilitud de los atributos de las especies (Song *et al.,* 2015). Sin embargo, más allá de estas diferencias y dada la urgente necesidad de mitigar el efecto antropogénico, el estudio de la diversidad funcional en el banco y la lluvia de semillas parece ser una estrategia viable para evaluar el efecto antropogénico sobre la regeneración natural y desarrollar indicadores que evalúen la integridad funcional de las comunidades.

ANTECEDENTES Y PLANTEAMIENTO DEL PROBLEMA

EL EFECTO ANTROPOGÉNICO SOBRE LOS BOSQUES TEMPLADOS DE MÉXICO

Los bosques templados de México se encuentran en zonas montañosas, entre los 1200 y 3600 m s.n.m., ocupan el 16% de su territorio nacional y están compuestos principalmente por bosques de pino, encino y oyamel (Challenger, 2003; Calderón de Rzedoswki y Rzedowski, 2001). En las regiones intertropicales como México, la presencia de los bosques templados se relaciona directamente con un efecto de altitud a partir de los 200 ms.n.m (Challenger, 1998). A diferencia de los bosques templados de mayores latitudes, en los cuales la temporada de lluvia se asocia con la estación de invierno, los bosques templados de México se distinguen por presentar una temporada de precipitación similar a la de los bosques tropicales (junio- octubre) (Challenger, 2003; Calderón de Rzedoswki y Rzedowski, 2001), condición que propicia una dinámica temporal particular y una alta diversidad de especies, tanto de origen neotropical como holártico (Calderón de Rzedowski and Rzedowski 2001; Challenger 2003; Cortés-Flores *et al.,* 2013; 2015). Actualmente se tiene registrado que los bosques templados de México albergan alrededor de 7,000 especies vegetales, que constituye el 24% de la flora estimada para el país (Calderón de Rzedowski y Rzedowski, 1991; Challenger, 2003; Merino, 2004). Por lo cual, los bosques templados de México son sistemas complejos de alta diversidad a través de los cuales se mantienen diferentes procesos (i, e., productividad primaria y captura de carbono) (Santibáñez-Andrade *et al.,* 2015), los cuales proveen bienes y servicios para el desarrollo humano, como la provisión de alimentos, agua y madera (Jujnovsky *et al.,* 2012).

A pesar de la importancia de los bosques templados de México, históricamente estos ecosistemas han sido sometidos a diferentes actividades como la ganadería intensiva y la deforestación (Merino, 2004; Castillo-Argüero *et al.,* 2016; Santibáñez-Andrade *et al.,* 2015). En esta situación, se promueve frecuentemente un régimen de disturbio crónico que generan gradientes, los cuales muestran zonas de menor a mayor perturbación y en los que se presenta más de un agente de disturbio con diferentes intensidades (Martorell and Peters 2005). En los bosques templados uno de los principales efectos inmediatos que pueden tener los disturbios crónicos es la pérdida de especies características (Santibáñez-Andrade *et al.,* 2015). Una

condición que a largo plazo modifica el ensamblaje de las especies y altera la función de estos ecosistemas (Pyšek, y Richardson, 2010; Mayfield *et al.,* 2010).

Si bien el desarrollo de indicadores ha demostrado ser una ser una herramienta eficiente, este enfoque no ha logrado determinar los efectos antropogénicos sobre el estado funcional de los bosques templados de México (Santibáñez-Andrade *et al.,* 2015). En la actualidad se tiene muy poco conocimiento acerca de cómo la pérdida de las especies características y la entrada de especies de malezas modifican los procesos de regeneración de los bosques templados y la integridad funcional (Santibáñez-Andrade *et al.,* 2015). El problema se agrava aún más si tomamos en cuenta que a nivel mundial no existen un consenso metodológico para el desarrollo de indicadores que evalúen los efectos de las especies de malezas a nivel funcional (Lavorel y Garnier, 2002; Mouillot *et al.,* 2007; Santibáñez-Andrade *et al.,* 2015).

El bosque templado de *Abies religiosa* de la Cuenca del río Magdalena (CRM) que forma parte del remanente de vegetación de la Ciudad de México (Santibáñez-Andrade *et al.,* 2015), ha sido un área expuesta a actividades como el turismo, la ganadería, la deforestación y el deshierbe (también conocido como chaponeo) (Santibáñez- Andrade *et al.,* 2015; Martínez-Orea *et al.,* 2019). En este bosque se ha demostrado que las actividades antropogénicas favorecen el éxito reproductivo y el establecimiento de las especies de malezas tanto de origen nativo como introducido (Martínez-Orea *et al.,* 2013; 2014; Santibáñez- Andrade *et al.,* 2015; Castillo-Argúero *et al.,* 2016; Martinez-Orea *et al.,* 2019). Las especies de malezas del bosque *de A. religiosa* presentan patrones fenológicos reproductivos asincrónicos con las especies características de la comunidad y promueven una tendencia adquisitiva de recursos bióticos y abióticos (Bonilla-Valencia *et al.,* 2017). Así mismo, diferentes estudios han demostrado que el deshierbe manual ha promovido cambios en las condiciones de luz que favorecen la germinación de malezas herbáceas, las cuales con el tiempo han dominado el sotobosque y han restringido la disponibilidad de sitios seguros para la germinación de muchas especies características (Martínez-Orea *et al.,* 2013; 2014; 2019). En este sentido, el bosque de *A. religiosa* de la CRM representa un excelente modelo de investigación para desarrollar indicadores ecológicos que evalúen el efecto antropogénico en la diversidad funcional.

OBJETIVO GENERAL

Realizar una evaluación del efecto de los disturbios antropogénicos sobre la integridad funcional del bosque templado de *A. religiosa* de la Cuenca del río Magdalena, Ciudad de México, utilizando un método que incorpora el desarrollo de indicadores funcionales.

OBJETIVOS PARTICULARES

- Establecer y caracterizar un gradiente de perturbación antropogénica en el bosque de *A. religiosa.*

- Generar una estrategia metodológica que permita desarrollar indicadores funcionales de respuesta a la intensidad del disturbio antropogénica y de su efecto sobre los cambios de composición.

- Integrar los indicadores ecológicos a través de un modelo de efecto causal y evaluar el efecto de los disturbios antropogénicos sobre la respuesta funcional de las especies características y malezas, y predecir los cambios del ensamblaje de especies en los procesos de regeneración natural.

HIPÓTESIS

De acuerdo con el efecto de los disturbios antropogénicos sobre la respuesta funcional de las especies se tienen tres hipótesis.

Hipótesis 0: Hipótesis nula

Mayores intensidades de disturbio antropogénico promueven la eliminación de especies características al azar en el ensamblaje de especie; bajo este escenario se espera que el decremento en la riqueza de especie reduzca la probabilidad de incluir atributos funcionales distintos (i.e., los disturbios antropogénicos no tienen un efecto en la modificación ambiental y en la sección de atributos funcionales). Por lo cual, en el bosque de *A. religiosa,* se espera que a mayor intensidad de disturbio antropogénico se observe un decremento en la riqueza de especies y la diversidad funcional (Figura 1 A).
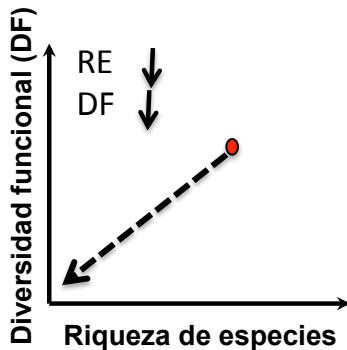
Hipótesis 1: Intensificación de los filtros ambientales

Mayores intensidades de disturbio antropogénicos ocasionan cambios ambientales que intensifican los filtros ambientales preexistentes; condición que promueven un efecto de convergencia funcional en el ensamblaje de especies, a través del incremento de especies de malezas con atributos y tolerancia similares a la perturbación. Por lo tanto, en el bosque de *A. religiosa,* se espera que mayores intensidades de disturbio antropogénico favorezcan el establecimiento de malezas con atributos funcionales similares entre ellas, y se observe un incremento de la riqueza a medida que se reduce la diversidad funcional (Figura 1 B).
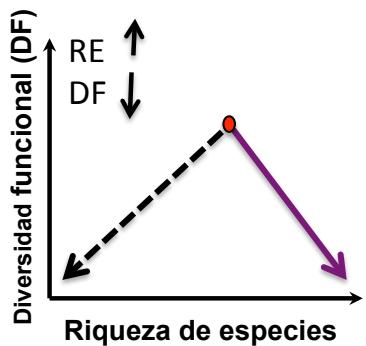
Hipótesis 2: Eliminación de filtros ambientales

Mayores intensidades de disturbios antropogénicos ocasionan la eliminación de filtros ambientales y la creación de nuevos nichos que promueven un efecto de divergencia funcional en el ensamblaje de especies; condición que favorece el establecimiento de especies de malezas introducidas con una alta variedad de atributos. Por lo tanto, en el bosque de *A. religiosa* se espera que mayores intensidades de disturbio antropogénico favorezcan la entrada de malezas con una alta variedad de atributos funcionales y se observe un incremento simultáneo de la riqueza de especies y la diversidad funcional (Figura 1 C).

A) Hipótesis 0

Diversidad funcional (DF)

RE
DF

Riqueza de especies

B) Hipótesis 1

Diversidad funcional (DF)

RE
DF

Riqueza de especies

C) Hipótesis 2

Diversidad funcional (DF)

RE
DF

Riqueza de especies
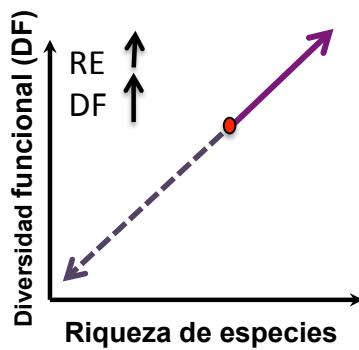
Figura 1. Graficas que representan las tres hipótesis planteadas del efecto del disturbio antropogénico sobre la riqueza de especies y la diversidad funcional. El punto rojo indica un estado conservado, la dirección de las flechas indica un estado de menor perturbación a uno de mayor perturbación antropogénica, la flechas con líneas puntuada representan las hipótesis 1 y las flechas moradas con líneas solidas representan las hipótesis 1 y 2 planteadas. **A) hipótesis 0: Hipótesis nula,** se espera que mayores intensidades de disturbio antropogénico promuevan un decremento de la riqueza de especies y la diversidad funcional. **Hipótesis 1: intensificación de filtros ambientales**, se espera que el incremento de los disturbios antropogénicos promueva intensificación de los filtros ambientales preexistentes y con ello el incremento de riqueza de especies de malezas con atributos funcionales similares entre ellas (mayor riqueza de especies y menor diversidad funcional). **Hipótesis 3: eliminación de filtros ambientales**, se espera que el incremento de la intensidad de los disturbios antropogénicos favorezca la riqueza de especies de malezas con una alta variedad de atributos funcionales (mayor riqueza de especies y diversidad funcional).

MÉTODO GENERAL

ÁREA DE ESTUDIO

BOSQUE DE *ABIES RELIGIOSA* DE LA CUENCA DEL RÍO MAGDALENA

El bosque de *A. religiosa* de la cuenca del río Magdalena (CRM), se localiza al suroeste de la Ciudad de México en la Sierra de las Cruces, dentro de la Faja Volcánica Transmexicana, en un intervalo de altitud entre 2,900 y 3650 m s.n.m. entre las coordenadas 19° 13' 53" N y 19° 18' 12" N y 99° 14' 50" N y 99° 20' 30" O y comprende un área de 1,071 ha (Figura 2, C). Se localiza al límite suroccidental de la Ciudad de México, que abarca las alcaldías Magdalena Contreras, Álvaro Obregón y Cuajimalpa (Figura 2 A y B) (Santibáñez-Andrade *et al.,* 2015). De acuerdo con la clasificación de Köppen, presenta un clima templado subhúmedo C (w_2) (w) b (i') (Álvarez, 2000). La temperatura media anual oscila entre los 13 °C, y la precipitación anual es de 950-1300 mm (Dobler-Morales, 2010).

El bosque de *A. religiosa* se desarrolla en un relieve montañoso con un ascenso continuo en altitud, que proviene de rocas ígneas extrusivas intermedias desarrolladas durante el Terciario Medio hasta el Plioceno (Lugo-Hubp, 1989; Álvarez, 2000). El suelo del bosque de *A. religiosa* es principalmente de tipo Andosol húmico, presenta en la superficie una capa oscura, rica en materia orgánica. Así mismo, dentro de este bosque sigue su curso el río Magdalena, el cual nace en las estribaciones de los cerros Palma, San Miguel, Cochinos y Coconetla, a una elevación aproximada de 3,650 m s.n.m. (Álvarez, 2000). De acuerdo con la vegetación, el estrato arbóreo es dominado por *A. religiosa,* con asociaciones con otras especies como *Pinus hartwegii* en zonas de mayor altitud y *Quercus rugosa* en áreas de menor altitud. El estrato arbustivo es dominado por *Salix paradoxa* y *S. nigra*. En el estrato herbáceo los géneros más representados son *Senecio, Salvia* y *Ageratina* (Santibáñez-Andrade, 2015).
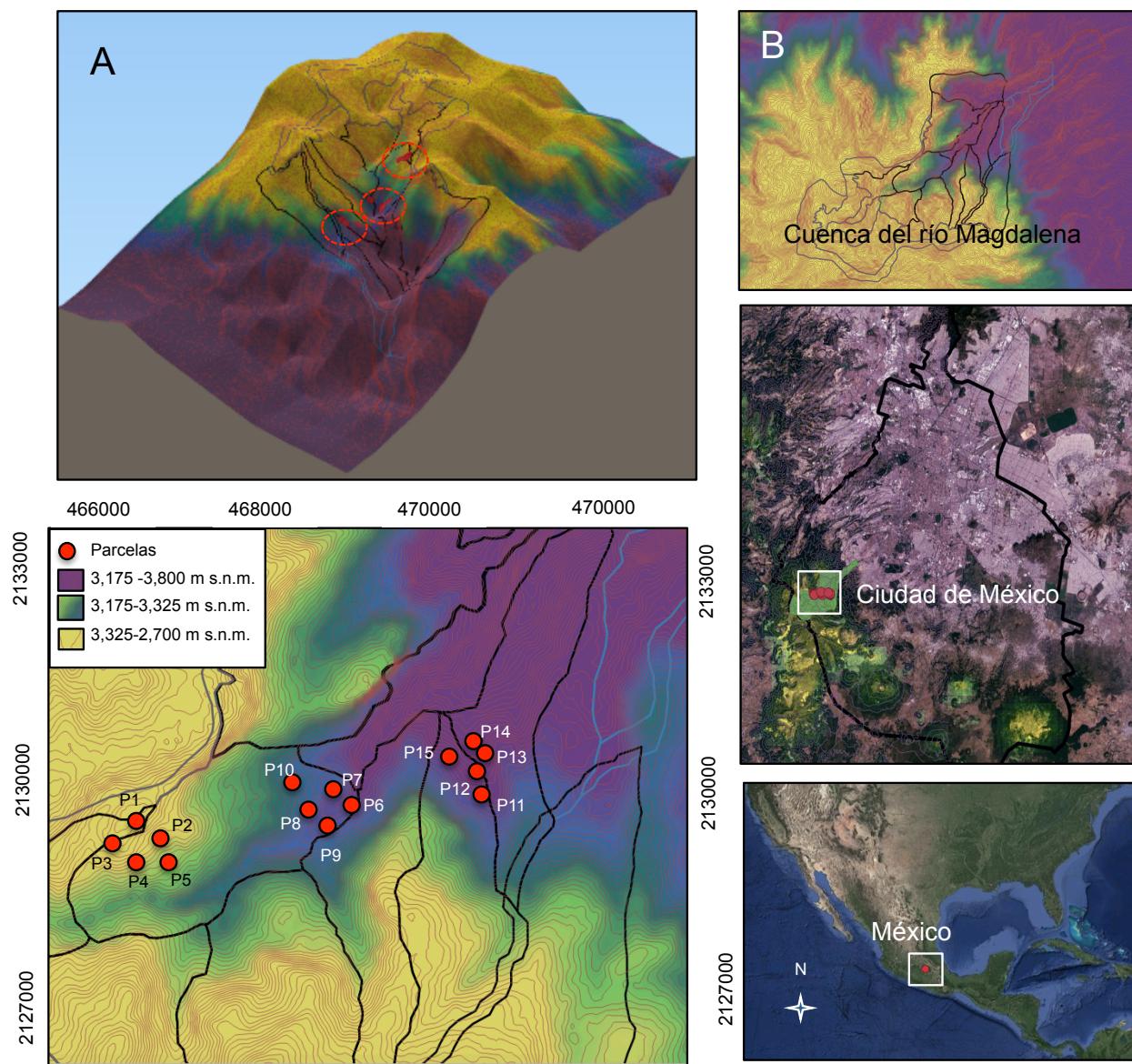
Figura 2. Localización de las parcelas de estudio en el bosque templado de *Abies religiosa* en la Cuenca del río Magdalena (CRM) de la Ciudad de México, México. **A.** muestra la localización de las parcelas y **B.** muestra la localización de la CRM.

ESTRATEGIA METODOLÓGICA

EVALUACIÓN DEL EFECTO ANTROPOGÉNICO SOBRE LA INTEGRIDAD FUNCIONAL

Para poder hacer una evaluación del efecto de los disturbios antropogénicos sobre la integridad funcional del bosque de *A. religiosa*, se desarrolló un marco teórico que demuestra la aplicación de la diversidad funcional como indicador ecológico y se realizó una propuesta metodológica para desarrollar estos indicadores.

En el capítulo 3 se desarrolla la propuesta metodológica denominada *"Inferencia lógica por abducción"* (Cuadro 1) que permite desarrollar indicadores ecológicos basados en la respuesta funcional de las especies a través de modelos de ecuaciones estructurales (SEM, por sus siglas en inglés Structural Equation Modeling). Este método se basa en una cadena causal, la cual se expresa en un modelo *a priori,* que considera que las perturbaciones antropogénicas y sus efectos sobre la modificación de diferentes variables ambientales (Figura 3 A, Flecha A) actúan primero como nuevos filtros de selección que favorecen las presencia de especies con atributos tolerantes; las cuales generalmente corresponden a especies de malezas y eliminan gradualmente la presencia de algunas especies características con atributos menos tolerantes (Figura 3 A , Flechas B1 y B2). Por lo tanto, a partir de este método es posible demostrar que las respuestas funcionales diferentes entre especies características y malezas son los conductores causales de los cambios de composición presentes en las comunidades (Figura 3 A, Flecha C1). Al considerar esta cadena causal, el método de *"Inferencia Lógica por Abducción"* desarrolla indicadores funcionales; a través de la selección por el Criterio de Información de Akaike (AIC) de la métrica funcional más plausible para explicar el efecto de los disturbios antropogénicos sobre la repuesta funcional de las especies y los cambios de composición, (Figura 3 A, Cuadro con líneas discontinuas).

Cuadro 1: *Inferencia Lógica por Abducción*

La *Inferencia Lógica por Abducción* es un razonamiento través del cual a partir de la descripción de un hecho o fenómeno (premisas = *p*) ofrece una explicación probable (hipótesis explicativa = *q*) considerando las premisas obtenidas (Bigelow, 2010).

En este estudio la *Inferencia Lógica por Abducción* considera como premisa verdadera la red causal de los efectos antropogénicos sobre la composición y la selección de un indicador funcional representa la búsqueda de la explicación más probable de la red causal.

El método de *"Inferencia Lógica por Abducción"* considera que, bajo condiciones de perturbación antropogénica, las diferencias entre las respuestas funcionales de especies de malezas y características y los cambios de composición (Figura 3 B, Flechas C2 y D1) son indicadores clave del estado funcional (Figura 3 B, Cuadros con líneas discontinuas). Por lo tanto, en el capítulo 4 se aplicó el método de *"Inferencia Lógica por Abducción"* para evaluar el efecto antropogénico sobre la integridad funcional en el bosque de *A. religiosa*. En este estudio se consideraron los atributos funcionales y los componentes de la vegetación asociados con la regeneración natural como el banco, la lluvia de semillas y la vegetación establecida; los cuales determinan directamente el mantenimiento de la integridad funcional a través del tiempo.
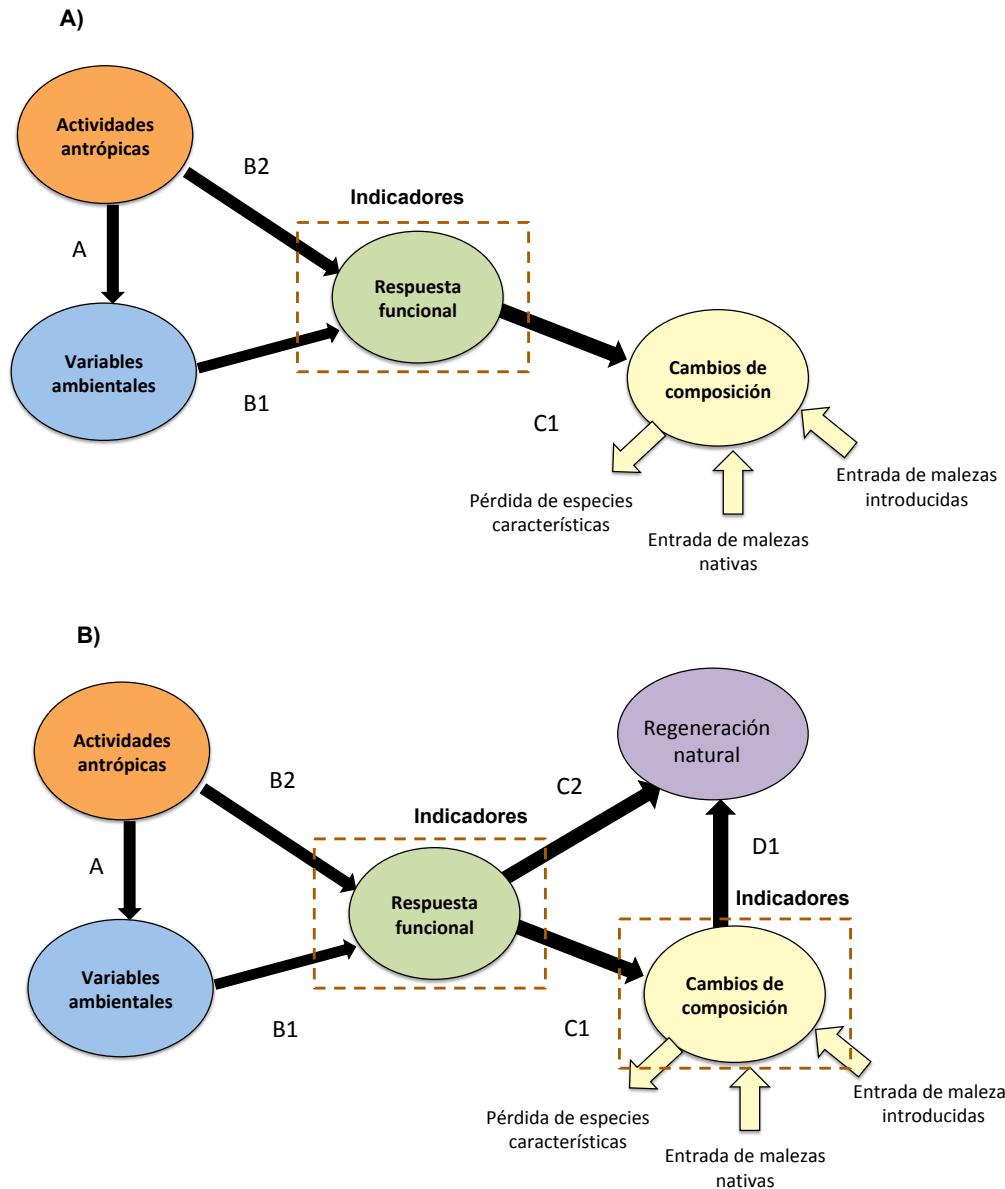
Figura 3. Esquema que muestra las relaciones causales del modelo *a priori* del efecto antropogénico. A) representa el modelo *a priori* para desarrollar el método de "*Inferencia por Abducción".* B) representa el modelo *a priori* para evaluar el efecto antropogénico sobre la integridad funcional del bosque templado de *Abies religiosa.* Las flechas negras representan los efectos causales en cada modelo *a priori.* Los cuadros con líneas discontinuas representan los indicadores desarrollados. La flecha A1 representa el efecto de los agentes de disturbio antropogénico en la intensificación y modificación de los filtros ambientales. Las flechas B1-B4 representan el efecto de los disturbios antropogénicos sobre los atributos de las especies características y malezas. La flecha C1 y C2 representan el efecto de las repuestas funcionales de las especies sobre los cambios de composición y sus efectos consecuentes sobre los procesos de regeneración natural. Subsecuentemente la flecha D2 representa el efecto de los cambios de composición sobre el mantenimiento de los procesos ecológicos.

Para poder hacer la evaluación de la integridad del bosque de *A. religiosa* se seleccionaron 15 parcelas de 30 × 30 m (13500 m^2 en total) de una gradiente de perturbación antropogénica, que se encuentran en tres cotas altitudinales en junio del 2018 (Figura 1 A) (altitud alta 2467-3449 m s.n.m., altitud media = 3202-3446 m s.n.m. y altitud baja = 3092-3122 m s.n.m). La selección de estas parcelas considero información previamente obtenida en los trabajos de Santibáñez-Andrade *et al.,* (2015) y Tovar Bustamante (2017). En las parcelas se determinaron tres indicadores de disturbio antropogénico; actividades de ganadería (AG), deterioro del hábitat (DH) y actividades humanas (AH). Los indicadores de disturbio antropogénico se obtuvieron por medio de una reducción de dimensiones con un análisis de componentes principales (PCA), siguiendo los métodos propuestos por Martorell y Peters (2005) con el programa estadístico R (v. 3.5.2; R Development Core Team, 2018). Los valores del índice del disturbio antropogénico (DI) y los indicadores para cada agente de disturbio antropogénico (AG, DH y HA) se muestran en la Figura 4. En esta grafica el índice de disturbio antropogénico (ID) representa la sumatoria de los tres indicadores de disturbio antropogénico y demuestra la presencia de un gradiente de disturbio en las parcelas seleccionadas. En la Figura 4 se observa que las DH y AG son las actividades que contribuyen mas en ID en comparación con HA. Posteriormente se desarrollaron indicadores ambientales e indicadores de vulnerabilidad de ensamblaje (i.e., composición, diversidad funcional y riqueza de especies) tanto en la vegetación como en el banco y la lluvia de semillas. Una vez obtenida esta información se evaluó la cadena causal de los disturbios antropogénicos sobre los indicadores de vulnerabilidad de ensamblaje mediante el método de *"Inferencia por Abducción".* La discusión de los resultados generados a través de la evaluación de la integridad funcional del bosque de *A. religiosa* es presentada en los capítulos 4 y el capítulo 5 de esta tesis.
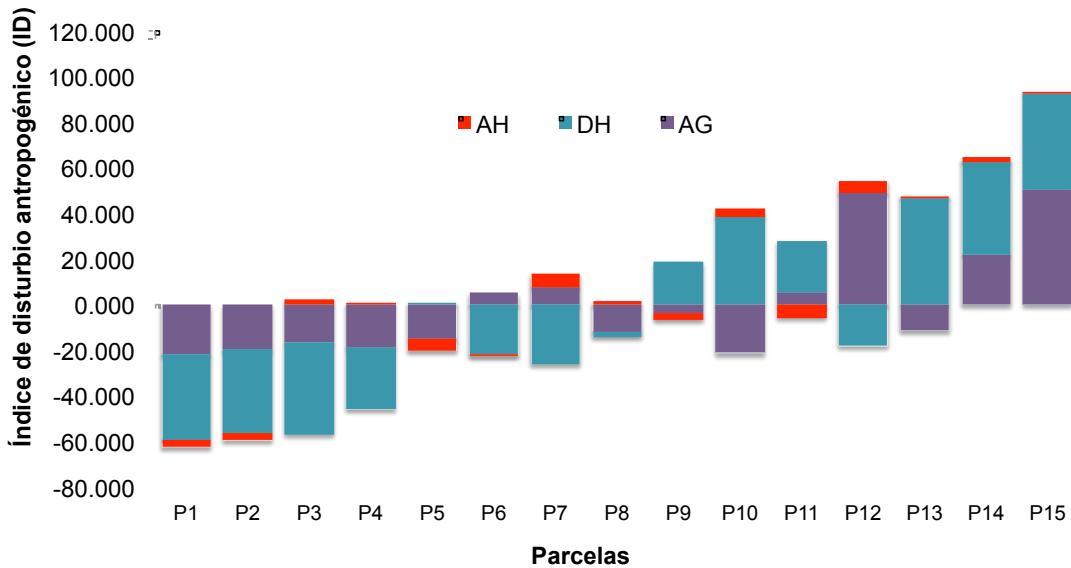
Figura 4. Índices de disturbio antropogénicos (ID) en cada parcela, los cuales representan sumatoria de los tres indicadores de disturbio antropogénico considerados, actividades de ganadería (AG), deterioro del hábitat (DH) y actividades humanas (AH). La gráfica muestra la presencia de un gradiente de perturbación antropogénico en las parcelas.

ESTRUCTURA DE LA TESIS

Capítulo 2. Linking functional diversity to ecological indicators; a tool to predict the anthropogenic effect on community functioning (Artículo de revisión).

A través de una revisión se muestra la aplicación de la diversidad funcional como indicador ecológico. Se demuestra que el efecto de los disturbios antropogénicos sobre la diversidad funcional depende de los cambios de composición, promovidos por el establecimiento de malezas. Por lo que se presentan evidencias de dos hipótesis acerca de los probables efectos que las especies de malezas pueden tener en la estructura funcional de las comunidades.

Capítulo 3. Functional indicators to explain the anthropic effects on community plant composition changes: The case of a temperate forest in Mexico (Artículo de investigación)

En este capítulo se presenta una propuesta metodológica denominada *"Inferencia lógica por abducción"* que permite desarrollar indicadores ecológicos basados en la respuesta funcional de las especies. Este método es desarrollado a través de modelos de ecuaciones estructurales (SEM) y permite seleccionar el indicador más plausible para explicar el efecto antropogénico sobre las repuestas funcional de las especies y sus consecuente efectos sobre los cambios de composición. En este capítulo se demuestra que las especies características y malezas tienen una contribución funcional diferente.

Capítulo 4. Predictions of the community assemblage in a temperate forest through indicators that evaluate the anthropogenic disturbance effect on natural regeneration (Artículo de investigación)

En este capítulo se aplica el método de "*Inferencia Lógica por Abducción* "en el bosque de *A. religiosa* de la CRM. En este trabajo se desarrollan indicadores de vulnerabilidad de ensamblaje (riqueza de especies, composición y diversidad funcional) que permitan evaluar el efecto antropogénico sobre la regeneración natural en el bosque de *A. religiosa* de la CRM. La aplicación de estos indicadores en la vegetación, el banco y la lluvia de semillas demostró que los disturbios antropogénicos promueven cambios en los procesos de regeneración natural que favorecen una entrada continua de malezas funcionalmente similares.

Linking functional diversity to ecological indicators; a tool to predict the anthropogenic effect on ecosystem functions

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Linking functional diversity to ecological indicators; a tool to predict the anthropogenic effect on ecosystem functions

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Abstract

Functional diversity is related to the maintenance of processes and functions in ecosystems. However, there is a lack of a conceptual framework that highlights the application of functional diversity as an ecological indicator. Therefore, we present a new initiative for motivating the development of ecological indicators based on functional diversity. We are interested in showing the challenges and solutions that these indicators imply. We integrated species assemblage theories and literature reviews. We considered plant traits related to ecosystem functions (specific leaf area, leaf dry matter content, wood density, phenology, and seed mass) to show the application of some functional diversity metrics as ecological indicators (i.e., Community weighted-mean, Functional divergence, Functional richness, and Functional evenness). We alert that functional diversity as an ecological indicator can be misinterpreted if species composition is unknown. Functional diversity values can be overrepresented by weed species (species established in disturbed sites) and do not maintain original processes and functions in ecosystems. Therefore, we search evidence to demonstrate that weed species are ecological indicators of functional diversity changes. We found support for two hypotheses that explain the effect of weed species on ecosystem function: functional homogenization and functional transformation. Likewise, we showed the application of some tools that can help study the anthropogenic effect on functional indicators. This review shows the paradigm of addressing the effect of anthropogenic disturbance on ecosystem processes through functional diversity, therefore represents an advance in developing ecological indicators that improve the environmental evaluation in areas under anthropogenic disturbance.

Keywords: weed species, leaf traits, seed mass, wood density, fruit and flower traits.

Introduction

At the global level, the use of ecological indicators for environmental evaluation and ecosystem conservation has expanded (Dale and Beyeler, 2001; Niemeijer and Groot, 2008; LaPaix et al. 2008; Müller et al. 2013; Tyler et al. 2021). Ecological indicators are quantitative and/or qualitative biological parameters that summarize complex information about the state of ecosystems (Niemeijer and Groot, 2008; Müller et al. 2013). However, one of the greatest challenges of ecological indicators has been to evaluate the anthropogenic effect on the functioning of the ecosystems, which is constituted by species, populations, and communities that have the full range of processes and the environmental conditions required to maintain them (Cardoso et al. 2013; Müller et al. 2013). Consequently, ecological indicators frequently incorporate different metrics to capture most of the possible complexity of ecosystem processes and often exceed the methodological efforts of management and conservation strategies (Rempel et al. 2016; Mora, 2019).

At present, a conceptual framework and new methodological strategies are required to develop ecological indicators that reduce the inherent complexity of the processes (LaPaix et al. 2009; Mason and Bello, 2013; Bonilla-Valencia et al. 2020; 2021). Approaches of functional diversity-based have demonstrated a direct linkage between species traits with the maintenance of ecosystem functions (i.e., pollination and regeneration) (Vandewalle et al. 2010; Mayfield et al. 2010a; Mouillot et al. 2013; Song et al. 2014; Glatthorn et al. 2021). Functional diversity is defined as the set of morphological, physiological, and phenological traits of species related to the maintenance of different ecosystem functions (Tilman et al. 1997; Díaz and Cabido, 2001; Song et al. 2014; Bonilla-Valencia et al. 2021). The term "function" (s) refers to the link that exists between different characteristics of community's species (traits) with ecosystem processes (Song et al. 2014; Glatthorn et al. 2021). Studying the diversity of functional traits has several advantages, such as having relatively easy measurement in the field and a range of values comparable between species (Zakharova et al. 2019). However, despite these characteristics, functional diversity is still a little-explored tool in developing ecological indicators. Most studies that evaluate the anthropic effect on functional diversity do not obtain conclusions about the

maintenance of these processes (Mayfield et al. 2010a; Mouillot et al. 2013; Bonilla-Valencia et al. 2020).

The lack of connection between the indicators theory with functional ecology has promoted a misinterpretation of functional diversity. For example the measures of high functional diversity are considered as indicators of a good conservation status (Freitas and Montovani, 2017). However, a large part of the functional measures may arise from weed species, which are higly competitive, either native or introduced species that establish, grow, and reproduce in highly disturbed areas, commonly by humans (Mayfield et al., 2010; Mouillot et al. 2013). Weed species frequently inhibit the establishment of characteristic species of a community (i.e., native species that evolved originally in the geographic region where they are) and modify the original functional traits of the community (Espinosa and Sarukhán 1997; Richardson et al. 2000; Drenovsky et al. 2012; Vibrans 2015). Therefore, from the perspective of ecological indicators, the entry of weed species is considered an indicator of possible changes in the original functional structure of a community (Mayfield et al. 2010a; Drenovsky et al. 2012; Ghazoul et al. 2015; Bonilla-Valencia et al. 2020; Ricciardi et al. 2021).

In this review, our main aim (1) is to demonstrate through the assembly theory and empirical evidence the application of functional diversity as an ecological indicator that describes species' response to anthropogenic disturbances and predicts the changes in ecosystems' functioning. We are interested in preventing the possible problems of interpreting functional diversity as an ecological indicator in areas that present weed species that potentially cause changes in the functional structure. Therefore, this review (2) demonstrates the main effects of the weed species on functional diversity and (3) shows some tools that improve the use of functional diversity as ecological indicators under perturbation areas with weed species.

Materials and Methods

In order to make this review, we realized a search for all existing published studies that demonstrate the linkage between the anthropogenic effects on the species functional response. For this, the searching terms were: "functional diversity" * "anthropogenic disturbance"; "functional trait *" anthropogenic* disturbance" (Science direct, Scopus and Google scholar dataset). We selected approximately 262 articles that evaluated the effect of anthropogenic activities on traits that directly contribute to ecosystem functions. In order to demonstrate the link between the functional response of species and the functional state of the ecosystem; we selected a set of traits related to (1) the survival response, reproduction, and growth of the plant's species (2) that play an important in weed species success. The selection of this set of attributes (3) is based on traits related to ecosystem functions widely demonstrated in the literature (Table 1). Such as leaf area (LA) and leaf dry matter content (LDMC; i.e., ratio of the fresh leaf weight dry leaf weight), specific leaf area (SLA; i.e., LA/LDMC ratio); traits that have been demonstrated to predict above-ground net primary production (aNPP) and soil litter decomposition rate in different ecosystems (Kazakou et al. 2006; Smart et al. 2017; Liu et al. 2018; Pakeman et al. 2011a; Hao et al. 2020). We consider wood density (i.e., ratio between dry mass of a wood and mass of water displaced by its green volume) due to its relation with aboveground biomass (AGB) and carbon capture and storage (Flores and Coomes, 2011; Theodorou et al. 2020). We consider flower and fruit type and color, flower and fruit syndromes, reproductive phenology traits related to pollination, dispersal, and natural regeneration (Pakeman and Eastwood, 2013; Warring et al. 2016; Theodorou et al. 2020). Seed mass also was considered as a functional trait due to its relationship with the germination rate and natural regeneration in different studies (Pakeman et al. 2013; Larson and Funk et al. 2016; Dyderski and Jagodzinski, 2018). We discard other traits used in the functional ecology, such as height and coverage, which are related to the structural complexity. Therefore, we review 35 articles to demonstrate the application of functional diversity metrics as ecological indicators, and we present them in three main parts. Part I explained the application of functional diversity metrics as ecological indicators through the assembly theory and the articles revised realized. Part II present various studies that showed the effect of weed species on functional diversity. Finally, part III includes some tools that could help develop ecological indicators based on functional diversity.

Part I. Functional diversity is an ecological indicator of anthropogenic disturbance effect

1.1 Anthropogenic disturbance and functional traits

In this paper, we find different studies that demonstrated that the functional traits respond to anthropogenic disturbance (Table 2). For example, it has been demonstrated that the increase of grazing, habitat deterioration, silviculture, and fragmentation promotes the decrease in the abundance of species with resource-conservation strategies with a high leaf dry matter content (LDMC). Conversely, these activities increased the abundance of species with a resource acquisition strategy with high specific leaf area values (SLA), and high nitrogen assimilation rate during photosynthesis (Mclntyre, 2008; Fortunel et al. 2009; Carreño-Rocabado et al. 2012; Dwyer et al. 2014; Bonilla-Valencia et al. 2020; Herben et al. 2017; Zeeman et al. 2018; Rodríguez-Alarcon et al. 2018). Consecutively, these changes promote losses of leaf diversity and an over representation of species with high specific leaf area values (SLA); that conduct to the community towards a functional homogenization through functional similarity (Rodríguez-Alarcon et al. 2018; Pakeman et al. 2011b; 2011c; Bonilla-Valencia et al. 2020) (Tables 1 and 3). At the ecosystem level, the changes in LDMC and SLA traits representation modify the litter decomposition rate (Kazakou et al. 2006; Liu et al., 2017) (Figure 1). Different empirical studies have shown, mainly in humid ecosystems, that the specific leaf area (SLA) and LDMC explained a large variation in the rate of leaf litter decoupling due to the difference in the decomposers abundance between these two types of leaves (Cornwell et al., 2008; Barbe et al. 2019; Xiao et al. 2020). Species with high SLA values composed of photosynthetic tissue (mesophyll) can more quickly decompose in the soil than species with high LDMC and sclerenchyma (dense tissues); leaf rich in (hemi) cellulose, insoluble sugars, and lignin, that maintain a slow decomposition rate (Kazakou et al. 2006; Pakeman et al. 2011a; Chen et al. 2019; Makkonen et al. 2013). Likewise, leaf traits diversity also has been demonstrated to have a positive and proportional relationship with the efficient use of resources among species and above-ground net primary production (aNPP) (Mason and de Bello, 2013; Smart et al. 2017; Hao et al. 2020). Therefore, in this study, the negative effects of livestock, land use, and fragmentation on diversity loss of leaf traits can be

considered as an indicator of above-ground net primary production (aNPP) losses (Rodríguez-Alarcon et al. 2018; Pakeman et al. 2011b; 2011c; Bonilla-Valencia et al. 2020)

1.2 Functional metrics as an ecological indicator

At present, there are different functional metrics available (Table 3) to quantify changes in the variety and abundance of attributes in species, through which the development of ecological indicators that explain the development of ecological indicators that explain the anthropogenic disturbance effect on ecosystem functions is possible (Garnier et al. 2004) (Figure 1). The application of these metrics as ecological indicators first requires the understanding of how the assemblage processes of environmental filters and competitive exclusion are modified in an anthropogenic context (Mouillot et al. 2007; Mayfield et al. 2010a). Secondly, it requires the understanding of the two main hypotheses that explain the relationship between functional diversity and ecosystem functioning; mass ratio hypothesis and niche complementarity effect hypothesis (Tilman et al. 1997; Grime, 1998; Song et al. 2015). Below we show how these hypotheses, and these metrics can be applied to the development of functional indicators.

1.2.1 Community Weighted-mean metric (CWM) as an ecological indicator

The theory of environmental filters considers that environmental conditions act as selection filters that favor the presence of species with certain traits that allow them to tolerate the conditions (for example, similar humidity and light requirements for germination) (Song et al. 2015; Kraft et al. 2015). Therefore, according to this hypothesis, we could expect that anthropogenic activities cause environmental changes that intensify and/or modify the pre-existing environmental filters and therefore shift the effects of selection towards a new set of traits (Mayfield et al. 2010a).In different ecosystems, it has been shown that the increase of anthropogenic disturbances (types, frequencies, and intensities) can promote trait over-representation due to the increase of the abundance of species with similar functional traits and tolerant to anthropogenic disturbances (e.g., functional convergence) (Mouillot et al. 2013). The anthropogenic effect on a dominant trait can evaluate through the community weighted-mean metric (CWM) (Table 3). CWM indicates the trait values that best represent the community species and determine the ecosystem

function (Garnier et al. 2004). This metric was developed considering "the mass ratio hypothesis," which predicts that dominant traits of a community determine the rate and magnitude of ecosystem processes and/or functions (Grime, 1998). We found, deforestation, some silviculture activities, and fragmentation promote the decrease of the abundance of tree species and the community weighted-mean metric of wood density (CWM-WD) (Carreño-Rocabado et al. 2012; Lin et al. 2015; Berenguer et al. 2018; Rodríguez-Alarcon et al. 2018; Fernandes-Neto et al. 2019). Consequently, this affects the aboveground biomass and the ecosystem carbon stock (Flores and Coomes, 2011; Bu et al. 2019) (Figure 1). Wood density describes the proportion of fiber tissue in the stem of each community's individual; thus, a community that presents a high dominance of tree individuals with a high proportion of fiber tissue have high CWM-WD values and can store higher carbon content per unit volume than species with lighter woods (Swenson et al. 2007).

1.2.2 Functional diversity metrics as ecological indicators

The theory of competitive exclusion predicts that communities will favor the functional difference of traits between species (patterns of functional divergence) due to the use of different resources in the ecosystem (Córdova-Tapia and Zambrano, 2015). For example, competition for pollinators and dispersers represents one of the main factors of competitive exclusion for species. This promotes the dissimilarity of reproductive traits (e.g., type and color of flowers) and the maintenance of different pollination interactions in the ecosystems (Johnson and Bronstein, 2019) (Figure 2). At present, the study of the variety of traits represents a way to know the state of the processes and functions in ecosystems. The niche complementary effect hypothesis proposes that the functional traits' dissimilarity between species favors a greater number of niches with differences in their efficient use of resources (Tilman, 1997). Therefore, we would expect that a greater variety of functional traits favors the maintenance of the ecosystem functions (Díaz and Cabido, 2001; Córdova-Tapia and Zambrano, 2015). However, under anthropogenic disturbance, competitive hierarchy assembly effects promote loss of traits; due to the effect of species with highly competitive traits, which will displace species with less competitive traits (Mayfield et al. 2010a; 2010b). We found fragmentation, land use, and urbanization promotes loss of species with reproductive traits associated with biotic pollination. Likewise, these activities favored

species with traits related to abiotic dispersal and pollination and similar germination requirements (Girão et al. 2007; Castro et al. 2010; Pakeman et al. 2011c; Pakeman and Eastwood et al. 2013; Sonnier et al. 2014; Pessoa et al. 2017; Herben et al. 2017: Fernandes-Neto et al. 2019; Hooper and Ashton, 2020; Theodorou et al. 2020), therefore affecting natural regeneration, the maintenance of crop productivity, promoting the shortage of a wide range of foods (Figure 1) (Pakeman and Eastwood, 2013; Warring et al. 2016; Theodorou et al. 2020). The development of indicators based on functional diversity is a viable strategy because there are different metrics available that determine the variety of traits in a community. Such as Functional richness (FRic), Functional evenness (FEve), Functional divergence (FDiv), and Functional dispersion (FDis) (Table 3); which were the metrics of functional diversity more frequent in the articles reviewed for this study. Also, there are databases that show the relationship of different traits with ecosystem functions, for example, LEDA (Knevel et al. 2003) and TRY databases (Kattge et al. 2011).

Part II. The interpretation of functional diversity as an ecological indicator depends on the species composition

One of the greatest challenges in implementing ecological indicators is the rigorous interpretation of each one of them (Niemeijer and Groot, 2008; LaPaix et al. 2008; Müller et al. 2013; Tyler et al. 20219). Interpretation of ecological indicators based on functional metrics highly depends on the species composition (Bonilla-Valencia et al., 2021). During the construction of these indicators, it is important to consider that contribution of species on ecosystem functions can be different between characteristic and weed species (Mayfield et al. 2010a). Characteristic species which are natives that evolved originally in a geographic region, present a great variety of functional attributes with adaptations to environmental regimes and natural disturbances that favor their continuous recruitment and the maintenance of the original processes over time (Espinosa and Sarukhán 1997; Richardson et al. 2000; Drenovsky et al. 2012; Vibrans 2015). For example, communities subjected to constant anthropogenic disturbances with impoverished vegetation, which show some characteristic species in the sources of natural regeneration (e.g., the rain and the seed bank), frequently promote the recovery of certain functions (Ghazoul et al.

2015; Ma et al. 2019; Bonilla-Valencia et al. 2021). Therefore, we would expect that under conditions of high anthropogenic disturbance, the loss of characteristic species richness promotes a proportional loss of ecosystem functions (as proposed in the sampling effect hypothesis) (Figure 1, A) (Song et al. 2014). However, this scenario rarely happens due to anthropogenic disturbances that can promote the losses of some characteristics species that are redundant functionally (i.e., species with similar functional traits) (Diaz and Cabido 2001; Bonilla-Valencia et al. 2021; Song et al., 2014). Therefore, eliminating those species probably does not affect certain ecosystem functions because the remaining species can compensate it (Diaz and Cabido 2001; Bonilla-Valencia et al. 2021).

Likewise, in addition to the loss of characteristic species, anthropogenic disturbances frequently promote environmental modifications that negatively affect the species assemblage and favor the entry of weed species (Mayfield et al., 2010). The weeds are native or introduced species highly competitive under disturbance that promotes modifications on the original functional structure (Espinosa and Sarukhán 1997; Richardson et al. 2000; Drenovsky et al. 2012; Vibrans 2015). In this review, we determined under which conditions of anthropogenic disturbances weed entry promote functional diversity changes. We found evidence of two hypotheses proposed by Mayfield et al. (2010a) about the effect of weed species on functional diversity under anthropogenic disturbance: (A) functional homogenization and (B) functional transformation. The hypothesis of functional homogenization predicts that anthropogenic disturbances can function as selection filters, promoting the elimination of characteristic species and the colonization of native and introduced weeds with similar and tolerant functional characters. Under this scenario, species richness increases, and functional diversity is reduced and homogenized (Mayfield et al. 2010a; Mouillot et al. 2013) (Figure 1, B). We found that grazing, fertilizer runoff, urbanization, and land use favor the presence of weed species with similar traits with high SLA associated to an acquisitive resource strategy (McIntyre, 2008; Dwyer et al. 2014; Zeeman et al. 2018; Bonilla-Valencia et al. 2020). This species also showed a high production of small seeds (<4 mm), wind-dispersed that commonly form persistent seed banks (Dyderski and Jagodzinski, 2018; Zeeman et al. 2018; Bonilla-Valencia et al. 2021; Waddell et al. 2020; Ficken and Rooney, 2020). Therefore, weed species probably modified some functions related to litter decomposition and natural regeneration (Table 1).

While the functional transformation hypothesis predicts that the anthropogenic disturbances can eliminate environmental filters and generate spatial and temporal niches for introduced weeds with functional traits different from those present in characteristic species; in this situation, the species richness and functional diversity are increased. (Figure 1, C) (Mayfield et al. 2010a; Wolkovich and Cleland 2010). We found that livestock, habitat degradation, and land use promote the entry of introduced weeds with phenological patterns different from those of characteristic species (Godoy et al. 2009; Bonilla-Valencia et al. 2021). Probably this can also increase the competitive advantages of weeds when using soil resources for building up flowers and fruits. Additionally, it can promote higher attraction to pollination and dispersal agents (Wolkovich and Cleland 2010; Lediuk et al. 2014). Therefore, during the development of ecological indicators, it is necessary to consider that the entry of new traits does not always represent a better functional conservation status in ecosystems. Although, the presence of weeds species is widely recognized as an indicator of potential functional changes, functional studies rarely report the effect of weed species on functional diversity (Helm et al. 2015; Bonilla-Valencia et al. 2020. In this review, we found that in most of these studies, species composition is not considered (Table 2). We propose the implementation of composition indicators to improve the interpretation of functional diversity as an ecological indicator (Ghazoul et al. 2015; Helm et al. 2015; Bonilla-Valencia et al. 2020).

Part III. Tools to improve the use of functional metrics as ecological indicators

We suggest that the application of functional diversity as a functional indicator requires prior knowledge of the community composition and the categorization of characteristic and weed species, due to the fact that it has a different functional contribution on the site where they are located. Knowing the richness and abundance of the characteristic species versus weed species can improve the understanding of functional diversity metrics as ecological indicators. Richness potentially provides information on the proportion of characteristic and weeds species that contribute to functional diversity. In comparison, abundance allows determining the proportion of abundance of characteristic and weed species that contribute to metrics such as the Weighted Mean Measure (CWM). Likewise, the integration of indicators that measure the proportion of

characteristic and weed species is possible through composition indicators. For example, the index of Favorable Conservation Status (FSC) describes the community composition through the relation between the abundance of characteristic species and introduced weed species (Helm et al. 2015). These metrics proved to be an efficient tool to predict the effect of weed species on ecosystem functions in temperate forests (Bonilla-Valencia et al. 2020; 2021). Likewise, the invasion risk index, which jointly weights the presence of weed species, can be a strategy to evaluate the effect of these species on a regional scale (del-Val et al. 2015). However, it is important to consider that the development of composition indicators requires identifying the species in the communities—an exhaustive task during the seed and seedling stages (Larson and Funk, 2016). Also, the sources of information for categorizing native and introduced species are often not always available for all species (Helm et al. 2015). Consequently, to advance the knowledge of community composition, future investigations of functional ecology will require interdisciplinary support with other branches, such as taxonomy, evolutionary ecology, and biogeography.

At present statistical procedures are required to evaluate the anthropogenic effects on composition and functional indicators. Structural Equation Models (SEMs) have demonstrated to be a powerful tool that allows the incorporation of the complexity of the causal network of the anthropogenic effect on regeneration processes (Santibáñez-Andrade et al. 2015; Fan et al. 2016; Zambrano et al. 2019; 2020; Bonilla-Valencia et al. 2020). Likewise, the package piecewiseSEM of R, recently developed, represents an advance in the SEMs (Lefcheck, 2016) because it allows modeling variables with a distribution different from the Gaussian and incorporating the use of generalized linear models (GLMs) (Bolker et al. 2009). However, it is essential to point out that SEMs are a confirmatory statistical technique that seeks to corroborate previously made hypotheses (Shipley 2002; Grace 2006). Therefore, we suggest a rigorous understanding of the study system to apply the indicators in the SEMs.

4. Final considerations

It is important to note that in this paper, only "soft" traits that are easy to measure were considered. However, many "hard" traits with a more difficult measurement can have a more

direct relationship with ecosystem processes and/or functions compared to "soft" traits (Lavorel and Garnier, 2002; Lozanovska et al. 2018; Zakharova et al. 2019). For example, the relative growth rate in plants is considered a "hard" trait and a direct indicator of the ecosystem's productivity, which has been replaced with a set of "soft" traits such as LA, SLA, and LDMC (Lavorel and Garnier, 2002; Lozanovska et al. 2018). However, there is no consensus on which traits should be used according to the perspectives of a particular research. Given the urgent need to stop and mitigate the impact of anthropogenic disturbances on nature, we suggest that applying "soft" traits is a viable strategy to reduce the costs and times of environmental assessment (Vandewalle et al. 2010).

Conclusions

This work shows the paradigm of addressing the ecosystem functions through functional diversity. Metrics such as the weighted-mean measure (CWM) and functional diversity metrics seem to be tangible tools to develop ecological indicators and to evaluate on a short time scale the functional contribution of species under conditions of anthropogenic disturbances. The proposal of these indicators also implies new challenges in order to relate functional diversity metrics with composition indicators. We expect that future research will develop functional indicators that predict the effect of the colonization of weeds on ecosystem function. The implementation of these indicators brings about the possibility of speeding up the evaluation of the anthropogenic disturbance effects on ecosystem functions and mitigating the impacts of weed species.

Author contributions
LBV, SCA, and YMO conceived the idea of proposing the functional metrics as ecological indicators. LBV carried out the search and synthesis of the literature. AZH, FJEG, and RLC provided information about the study of weed species and anthropogenic impacts. All authors participated in the manuscript.

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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Tables

Table 1. Relationship among functional trait sets with ecosystem functions. The references demonstrated the relationship of the traits with ecosystem functions. LA= leaf area, SLA= specific leaf area, LDMC= leaf dry matter content. LDMC; ratio of the fresh leaf weight dry leaf weight, SLA; ratio LA/LDMC, wood density; ratio dry mass of a wood / mass of water displaced by its green volume.

Trait	Functional trait	Ecosystem functions	References
Leaf traits	LA SLA LDMC	Litter decomposition rate	Kazakou et al. (2006) Pakeman et al. (2011a) Liu et al. (2017)
	LA SLA LDMC	Above- ground net primary production (aNPP)	Mason and de Bello (2016) Smart et al. (2017) Hao et al. (2020)
Wood trait	Wood density	Above-ground biomass (AGB)	Bu et al. (2019)
	Wood density	Carbon capture and storage	Flores and Coomes (2011)
Reproductive trait and seed traits	Pollen vector type Flower color	Pollination	Theodorou et al. (2020)
	Dispersal Syndrome Fruit phenology Fruit color Seed size	Dispersal	Warring et al. (2016)
	Pollination syndrome Flower phenology Dispersal Syndrome Fruit phenology Seed mass	Natural regeneration	Pakeman and Eastwood (2013)

Table 2. Functional indicators based of functional metrics. The references demonstrated the application of metrics as ecological indicators to anthropogenic disturbance in different traits sets. LA= leaf area, SLA= specific leaf area, LDMC= leaf dry matter content. ***Indicates** functional changes promoted by weed and introduced species. CWM = Community weighted-mean, FRic = Functional richness, FDiv = Functional divergence, FEve = Functional evenness, FDis =Functional dispersion. Rao index= reflects changes in the abundance-weighted sum of pairwise functional distances between species. FD= Mason's index of functional diversity.

Trait	Functional trait	Indicator (Metric)	Anthropogenic disturbance	Reference
Leaf traits	SLA LDMC	NA	Grazing and fertilizing	* McIntyre (2008)
	SLA	NA	Fertilizer runoff	*Dwyer et al. (2014)
	LA SLA LDMC	CWM FDis	Grazing and habitat deterioration	*Bonilla-Valencia et al. (2020)
	SLA	NA	Urbanization	*Zeeman et al. (2018)
	LDMC	NA	Land use	Fortunel et al. (2009)
	SLA LDMC	FRic FEve FDiv FDis	Land use	Pakeman et al. (2011b)
	SLA LDMC	CWM FD	Land use	Pakeman et al. (2011c)
	SLA LDMC	CWM	Silviculture	Carreño-Rocabado et al. (2012)
	SLA	NA	Logging, cutting, mowing, herbivory	Herben et al. (2017)
	SLA LDMC	CWM FRic FEve FDiv FDis	Fragmentation	Rodríguez-Alarcon et al. (2018)
	SLA LDMC	CWM	Pasture and clear-cut	Fernandes-Neto et al. (2019)

Table 2. Continued

Trait	Functional trait	Indicator (Metric)	Anthropogenic disturbance	Reference
Wood trait	Wood density	CWM	Silviculture	Carreño-Rocabado et al. (2012)
	Wood density	CWM	Deforestation	Lin et al. (2015)
	Wood density	NA	Selective logging, Understory fires, Fragmentation	Berenguer et al. (2018)
	Wood density	CWM	Fragmentation	Rodríguez-Alarcon et al. (2018)
	Wood density	CWM	Pasture and clear-cut,	Fernandes-Neto et al. (2019)
Reproductive traits	Flower phenology	NA	Habitat deterioration	* Godoy et al. (2009)
	Pollination syndromes Flower phenology Dispersal Syndrome Fruit phenology Seed mass	FDiv	Grazing livestock Habitat deterioration	*Bonilla-Valencia et al. (2021)
	Flower size Flower rewards Flower type	NA	Fragmentation	Girão et al. (2007)
	Pollination vector Dispersal vector	NA	Land use	Castro et al. (2010)

Table 2. Continued

Trait	Functional trait	Indicator (Metric)	Anthropogenic disturbance	Reference
Reproductive traits	Flower phenology (start and end)	CWM FD	Land use	Pakeman et al. (2011c)
	Flower phenology Pollen vector type	CWM FRic FEve FDiv	Land use	Pakeman and Eastwood (2013)
	Fruit diameter Fruit length Fresh pulp	FRic FEve FDiv CWM	Deforestation	Pessoa et al. (2017)
	Pollination vector	FRic FEve FDiv	Fragmentation	Hooper and Ashton (2020)
	Flower color Flower shape	Rao	Fragmentation	Theodorou et al. (2020)
Seed traits	Seed mass	CMW	Land use	* Dyderski and Jagodzinski (2018)
	Seed mass	NA	Urbanization	* Zeeman et al. (2018)
	Seed mass Dispersal syndrome	CWM	Land use	* Waddell et al. (2020)
	Seed mass	NA	Land use Grazing Fire	*Ficken and Rooney (2020)

Table 2. Continued

Trait	Functional trait	Indicator (Metric)	Anthropogenic disturbance	Reference
Seed traits	Seed mass	NA	Land use	Castro et al. (2010)
	Seed mass	CWM FD	Land use	Pakeman et al. (2011c)
	Seed longevity Seed mass	CWM FRic FEve FDiv	Land use	Pakeman and Eastwood (2013)
	Seed bank Seed bank capacity	FRic	Fragmentation	Sonnier et al. (2014)
	Seed diameter Seed length Seed weight	FRic FEve FDiv CWM	Deforestation	Pessoa et al. (2017)
	Seed mass	NA	Logging, cutting, mowing, herbivory	Herben et al. (2017)
	Seed mass	CWM	Fragmentation	Fernandes-Neto et al. (2019)
	Seed size category Seed dispersal syndrome	FRic FEve FDiv	Fragmentation	Hooper and Ashton (2020)

Table 3. Description and explanation of the possible values of functional diversity metrics, reference that shows its detailed construction.

Indicator (Metric)	Description	Unit	Explication	Reference
Community weighted-mean (CWM)	The mean value of traits across species weighted by their abundance.	NA	The mean value increases, as the value of the most dominant trait, increases.	Garnier et al. (2004)
Functional richness (FRic)	Amount of functional space occupied by species in the community.	NA	FRic increases as potentially used functional space increases.	Villéger et al. (2008)
Functional divergence (FDiv)	The variance of the traits, weighted by the abundances of the species.	(0 to 1)	Values close to 0 indicate that the most dominant species have similar trait values. In contrast, values close to 1 indicate that the most dominant species have extreme traits values in the functional space.	Villéger et al. (2008)
Functional evenness (FEve)	Quantifies the evenness of the distribution of the relative abundances of the traits.	(0 to 1)	Values close to 0 indicate few dominant species with similar functional values. In contrast values close to 1 indicate that the species are equally abundant and functionally equidistant.	Villéger et al. (2008)
Functional dispersion (FDis)	Changes in the deviation weighted by the abundances of the traits of the species, from the center of the functional space.	NA	FDis increases as the deviation from the center of the functional space increases	Laliberte and Legendre (2010)

Anthropogenic disturbances

Explanation

Ecological indicator (trait)

LA
SLA
LDMC

Wood density

Pollination syndrome
Flower phenology
Flower color
Dispersal Syndrome
Fruit phenology
Fruit color
Seed mass

Composition changes

Ecosystem Functions

Litter decomposition rate
Above-ground net primary production (aNPP)

Above-ground biomass (AGB)
Carbon capture storage

Pollination
Dispersal
Natural regeneration

Functional diversity

A)Sampling effect hypothesis
Proportional loss of species and functional diversity.

B) Functional homogenization hypothesis
Increase of weed species with similar traits.

C) Functional transformation hypothesis
Increase of weed species with different traits.

Species richness

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Figure 1. The scheme explains the effect of anthropogenic disturbances on ecological indicators based on species traits, which predict changes in ecosystem processes. The green arrows represent the anthropogenic effect on species traits; the orange arrows represent the subsequent effect on ecosystem processes. Curved arrows explain the anthropic effect on composition changes in a community and their subsequent impacts on ecosystem processes (hypotheses originally made by Mayfield et al. 2010a). Graphs show the hypotheses of the effects of increased anthropogenic disturbances on species richness and functional diversity. The large red circle represents the state of the community before anthropogenic disturbance, and the direction of the arrow represents changes in species richness and functional diversity as the intensity of anthropogenic disturbance increases (indicated by the length of the arrow). A) Hypothesis according to the sampling effect; the increase in anthropogenic disturbances leads to a proportional loss of species richness and functional diversity. B) Hypothesis of functional homogenization; the increase of anthropogenic disturbances promotes the entry of native and introduced weed species with similar functional characteristics. C) Hypothesis of functional transformation; the increase of anthropogenic disturbance promotes the entry of introduced weeds with functional traits different from those of the characteristic species of the community. LA = leaf area, SLA = specific leaf area, LDMC = leaf dry matter content.
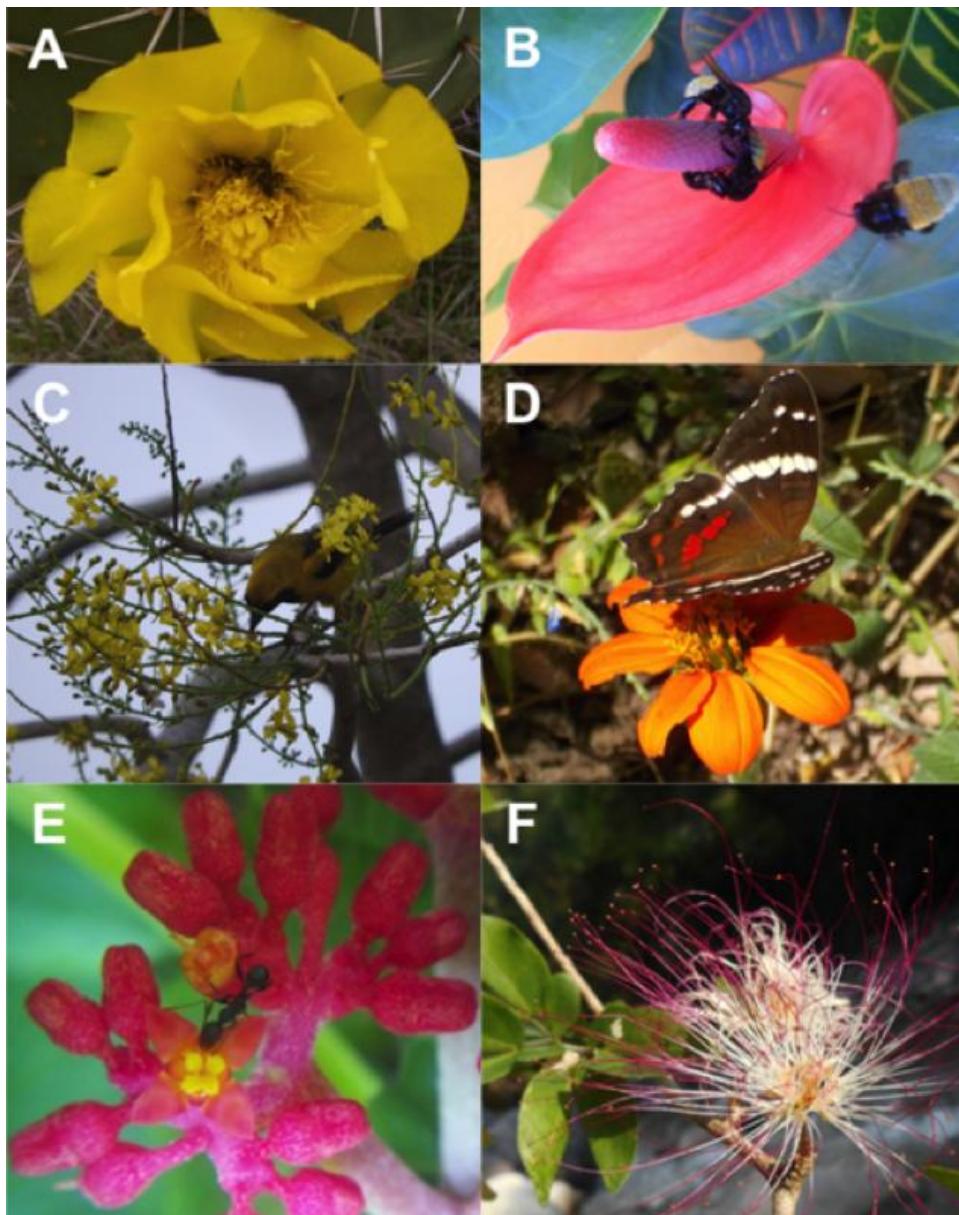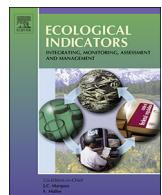
Figure 2. The diversity of floral traits directly influences the number of pollination interactions in an ecosystem. Floral characters are associated with their pollination syndromes. **A.** *Opuntia robusta* flowers visited by bees, **B.** Anthurium flowers visited by bumblebees, **C.** Flowers of the Papilionoidea superfamily visited by birds, **D.** Asteraceae flowers visited by butterflies, **E.** Flowers of the Vitaceae family visited by ants, **F.** flowers of the Mimosaceae family, with flowers without perianth wind pollinated (Photographic material by Sandra Ríos-Carrasco and Cesar Adrián González-Martínez).

Functional indicators to explain the anthropic effects on community plant composition changes: the case of a temperate forest in Mexico

Functional indicators to explain the anthropic effects on community plant composition changes: The case of a temperate forest in Mexico

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ABSTRACT

In plant communities, changes in composition driven by the dominance of weed species have been used as ecological indicators to predict the anthropic impacts on these species. Nevertheless, anthropic disturbances do not act directly on species composition, but their effects depend on the species' functional responses. Hence, anthropic effects follow a logical sequence, in which disturbances act at different levels. In order to understand the sequence of the changes in the community there is a need to develop functional and compositional integrated indicators. In order to integrate them we suggest a method based on inference by abduction, to reduce the complexity in predicting the anthropic effects on species functional responses. With this method we develop functional indicators of responses to anthropic disturbances and the effect on composition changes. The method involves building structural equation models (SEMs), through which we evaluate the anthropic and environmental effects on the functional response of species and composition changes in an integral way. From these causal paths, we select the best-fitting model with plausible functional indicators to explain the anthropic effects, according to Akaike's information criterion (AIC). This research develops a methodological proposal to build up functional indicators with foliar attributes associated to resource acquisition and use strategies of herb and shrub species in the temperate *Abies religiosa* forest in the Magdalena river basin in Mexico City. The built indicators demonstrate for the first time and in a simultaneous way, that characteristic species (original component) and native weeds (component established under perturbation conditions) have different responses to anthropic perturbations as well as different contributions to community composition changes. This result represents a methodological contribution in the evaluation of anthropic impacts and the use of native weed species as functional indicators.

1. Introduction

At the global level, anthropic disturbances have modified the composition and function of plant communities at an unprecedented speed, a condition that has favored the establishment of weed species (Chapin et al., 2000). Weeds are native or introduced species that are highly competitive under certain regimes of anthropic disturbance, which can increase their abundances and can even inhibit the growth of some characteristic forest species (i.e., species that evolved originally in the site where they are) (Richardson et al., 2000; Drenovsky et al., 2012). As a consequence some composition indicators have been

developed, for example Helm et al. (2015) and Santibáñez-Andrade et al. (2015) elaborated indicators based on the relation between characteristic and weed species abundance as a measure of the magnitude of anthropic disturbance and habitat change, however they did not consider the functional responses of species and the consequences of this at the compositional level in the community. Though there are currently different functional indicators that are based on a variety of biological attributes; they do not capture the causality of the anthropic effect at functional and composition levels, (review studies by Díaz et al., 2007; Duflot et al., 2014; and Capmourteres and Anand, 2016). Thus, functional indicators that enhance the understanding of anthropic

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effects on functional responses between characteristic and weed species need to be developed so that their differences and role as perturbation indicators are better understood (Drenovsky et al., 2012; Bruno, 2016).

Although composition indicators have demonstrated to represent the increase of anthropic activities (Helm et al., 2015), it is important to consider that anthropic disturbances do not act directly on species composition (Tilman et al., 1997; Song et al., 2014; Mayfield et al., 2010). First, continuous low-impact activities (chronic disturbances), such as constant livestock raising and the gradual loss of plant cover, cause environmental changes that intensify and/or modify preexisting environmental filters from local to microsite scales (Martorell and Peters, 2005; Martínez-Blancas et al., 2018). Thus, communities result from a hierarchy of successive filters, which select species with disturbance-tolerant attributes that frequently correspond to pioneer species and/or weeds (Richardson et al., 2000; Mayfield et al., 2010). Therefore, high intensities of anthropic disturbance and changes in composition will be promoted, which will favor a high abundance of weeds (Mouillot et al., 2013; Santibáñez-Andrade et al., 2015).

Due to the lack of functional indicators that consider the complexity of anthropic effects (Lavorel and Garnier, 2002; Lin et al., 2009; Mayfield et al., 2010), we present a methodological proposal for the development of indicators that evaluate, in an integral and simultaneous way, the anthropic effects on the functional responses of characteristic and weed species. The selection of functional indicators is performed through the inference of reasoning by abduction (Bigelow, 2010). This reasoning process allows in a practical way, through a group of previously selected variables, the detection of the most plausible indicators that connect causal pathways of the anthropic effect on the composition (Bigelow, 2010).

The aims of this study were (a) to corroborate through the application of SEMs whether the characteristic species and native weeds show similar functional responses to anthropic perturbations, due to their common adaptive history as we hypothesized or do they present different tolerance intervals, (b) to determine if the functional responses between characteristic species and weeds are the same in herbaceous and shrub species. We expect higher values of leaf area (LA) and specific leaf area (SLA) in herbaceous weeds than in shrub species due to resource acquisition strategy (Feng et al., 2008; Drenovsky et al., 2012). While shrub weeds will be associated with resource conservation strategy, attributes such as thick leaves with a high leaf dry matter content (LDMC) (Castro-Díez et al., 2002; Funk et al., 2016). Finally, (c) we evaluate the functional responses of characteristic and weed species and the implications of their use as anthropic perturbation indicators.

2. Materials and methods

2.1. Functional indicators method

2.1.1. Explanation of the inference by abduction method

The development of functional indicators represents an exhaustive task if we consider that there is a large number of available functional metrics (Mayfield et al., 2010; Mouillot et al., 2013). However, due to the logical sequence that the anthropic perturbations have on composition (Fig. 1), it is possible to use a logical reasoning of inference by abduction, which from a detected phenomenon (true premise), it is possible to give a causal probable explanation (probable premise) (Fitzhugh, 2008; Bigelow, 2010). This logical reasoning has been broadly used in medical and social sciences (Fitzhugh, 2008; Bigelow, 2010). In this study, inference by abduction is a logical process, which considers the anthropic and environmental effects on species function and composition as a premise (Fig. 1) and the anthropic effects on the functional response of species as a probable explanation (Fig. 1, B1-B4). Given the logical sequence of the anthropic effect on the functional response of the species (Fig. 1, B1-B4) and its subsequent effect on composition (Fig. 1, C1 and C2) (Lavorel and Garnier, 2002; Mayfield et al., 2010). From this reasoning, we used a two-step method to obtain
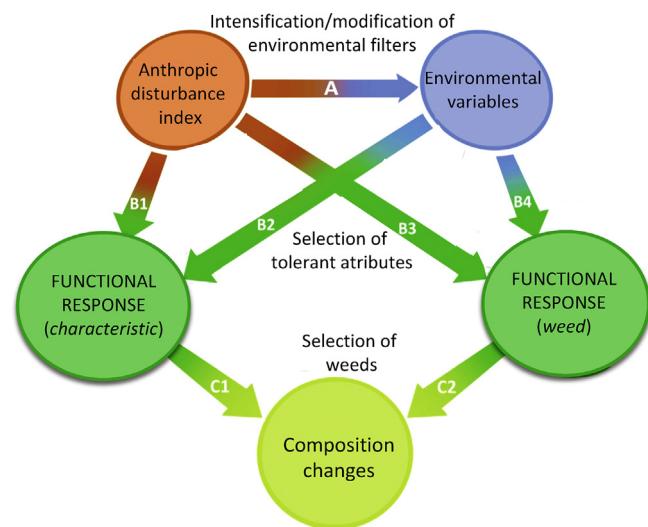
Fig. 1. Conceptual model of anthropic and environmental effects on species functional response and their effects on the changes in species composition of a community. Arrow A represents the effect of the anthropic disturbance agents in the intensification and modification of the environmental filters, through which the changes in environmental variables are promoted. Arrows B1, B2, B3 and B4 represent the effect of anthropic perturbations on the selection of attributes that confer tolerance to species; these are reflected in the functional responses of the species. Arrows C1 and C2 represent the effects of the functional responses on the probable selection of weed species that are represented in the composition changes.

functional indicators, which were used in our study system and further discussed. This method applied the inference by abduction through structural equation models (SEMs) to estimate the anthropic multiple effect causal pathways and to select functional indicators through Akaike's information criterion (AIC).

2.1.2. Step 1. Anthropic effect on the environment
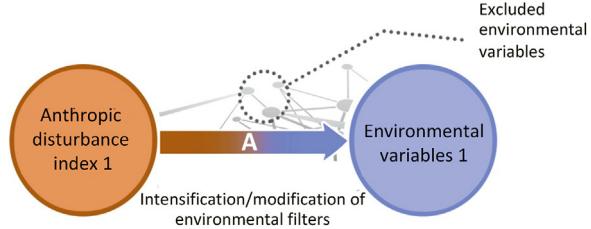
Given that human activities can modify preexisting environmental filters, an initial step is to corroborate the anthropic effects on the environmental factors (Fig. 2, arrow A) (Díaz et al., 2007). For this, we suggest fitting the total set of potential linear models, thus evaluating all potential effects of the anthropic disturbance agents (explanatory variables; fixed effects) on the environmental variables (response variables). Depending on the nature of the data, different models can be included: linear models (LMs; fixed effects), linear mixed models (LMMs; fixed and random effects), generalized linear models (GLMs; error distributions different from Gaussian) and generalized linear mixed models (GLMMs; fixed and random effects, and error distributions different from Gaussian) (Bolker et al., 2009). Afterwards, we suggest the selection of the best-supported models through the smallest Akaike's information criterion (AIC), evaluating the difference in the AIC value of each model with respect to the best-supported model (ΔAIC) (Burnham and Anderson, 2002; Lefcheck, 2016; Fig. 2, Step 1). The selected models thus include the disturbance agent and the environmental variables that will be evaluated in the next step (Fig. 2, Step 1 towards Step 2).

2.1.3. Step 2. Inference by abduction

Based on the logic of the inference by abduction and taking into consideration as a true premise the causal web of the anthropic effects on composition (Fig. 2), the search for a functional indicator (Fig. 2, arrows B1-B4) represents a likely key link in this web. To determine functional indicators, we propose fitting the total set of potential structural equation models (SEMs), representing the web of effects of the disturbance agents (exogenous predictors) and the environmental variables (endogenous predictors) on the species functional responses

Step 1: Antropic effect on the environment

LMM: selection of models with smallest AIC

Step 2: Inference by abduction

SEM: selection of models with smallest AIC
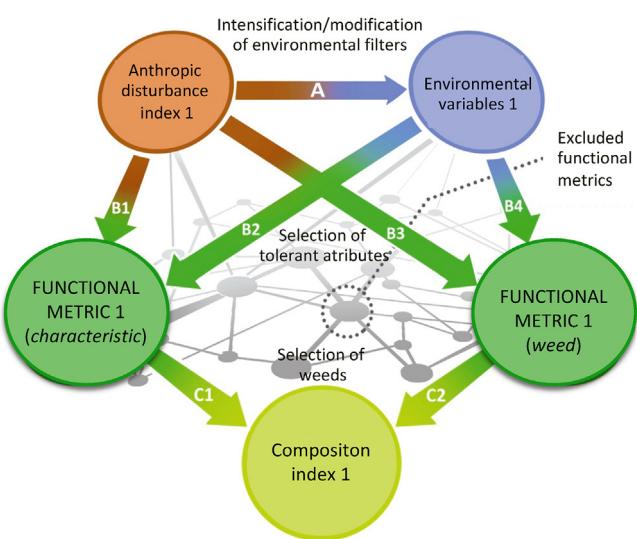
Fig. 2. Representation of the method for developing functional indicators of the response to disturbances and effect on composition changes. LMM = linear mixed model, SEM = structural equation model. AIC = Akaike's information criterion.

(endogenous responses) and the resulting changes in composition (exogenous composition response) (Fig. 2, Step 2). After estimating the total set of SEMs models, with different functional responses (attributes), the best -supported model would be selected through the AIC. In this way this model includes the functional response (attribute) that the functional indicator shows, and therefore that better explained the anthropic effect (Fig. 2, Step 2). SEM modeling can be performed with the statistical software piecewiseSEM (Lefcheck, 2016) on the statistical software R 3.5.2 (R Development Core Team, 2018). PiecewiseSEM allows to fit the models described in step 1 in a SEM context and to obtain AIC values from each SEM model, through nested comparison between models (including the missing functional metrics) (Lefcheck, 2016).

2.2. Application of the proposed method of functional indicators in the study system

2.2.1. Functional indicators method application

The application of the proposed method and the development of functional indicators was based on foliar attributes associated with the use and conservation of resources. This study was carried out in the understory community of an *Abies religiosa* forest. In the following paragraphs we describe the application of our proposed method.

2.2.2. Study site

The study was carried out in the temperate *Abies religiosa* forest in the Magdalena river basin, located southwest of the Valley of Mexico between 2900 and 3650 m a.s.l. and between 19° 13′ 53″, 19° 18′ 12″ N and 99° 14′ 50″, 99° 20′ 30″ W. The forest covers 3100 ha (Fig. 3, A and B) and adjoins a *Quercus* spp. forest at the lowest altitude (2700–2900 m s.n.m.), and at the highest altitudes, a *Pinus hartwegii* forest (Santibáñez-Andrade et al., 2015).

The *A. religiosa* forest has a temperate subhumid climate (C (w₂) (w) b(i')) with temperatures of 6 °C to 20 °C and a mean temperature of 13 °C. The annual precipitation ranges from 950 to 1300 mm. The season with the highest precipitation is from June to October (rainy season) and the lowest precipitation occurs from November to May (dry season) (Dobler-Morales, 2010). The forest canopy is between 20 and 40 m high with *A. religiosa, Sambus nigra* subsp. *canadensis* and *Salix paradoxa* as dominant species, while the understory is 2 to 3 m high, with species of *Senecio, Acaena, Salvia* and *Ageratina*. This forest is part of the conservation area of Mexico City; however, it experiences constant disturbances such as deforestation, livestock raising and weeding as a silvicultural practice (Santibáñez-Andrade et al., 2015).

2.2.3. Selection of the study plots

In the *A. religiosa* forest of the Magdalena river basin, in June 2017, we selected 15 30 × 30 m plots (13500 m² total) (Fig. 3, A). These plots were distributed along an anthropic perturbation gradient at three altitudinal levels (high altitude = 2467–3449 m a.s.l. plots 1–5; intermediate altitude = 3202–3446 m a.s.l., plots 6–10 and low altitude = 3092–3122 m a.s.l., plots 11–15). The selection of these plots was based on the characterization of the study site made by Santibáñez-Andrade et al. (2015) and Tovar-Bustamante (2017), as well as on environmental anthropic disturbance information obtained in May 2017.

2.2.4. Characterization of the anthropic disturbance gradient

In June 2017, in each plot, we determined the intensity of 11 anthropic disturbances due to three factors: livestock raising (LR), human activities (HA) and habitat deterioration (HD) (Table 1). For LR, we quantified the number of square m with livestock dropping (livdro), livestock roads (livroa), branched plants (brapla) and soil compaction (soicom). This last measurement was determined through the apparent density, which refers to the reduction in soil pores per volume unit (g/cm³) due to constant livestock trampling. In each plot, we randomly collected three soil samples with a cylinder (106.02 cm³), and the samples were oven dried (105 °C) for 24 h and then weighed. The apparent density was obtained using Keller and Håkansson's (2010) equation:

$$AD = 100 Ds/V, \tag{1}$$

where AD is the apparent density (g/cm³), Ds is the dry soil weight (g) and V is the cylinder volume (cm³).

For HD, we quantified the number of square meters that were subjected to weeding (weedin), deforestation (defore) and canopy openness (canope). The last factor was determined by 16 hemispherical photographs (digital camera Nikon D80, fisheye lens EX SIGMA4.5 2:28 DCHSM, Tokyo, JP). These were analyzed with the Gap Light Analyzer (GLA, 2.0) software, which quantifies the fraction of canopy openness (FAD) (GLA, 2.0; Frazer et al. 1999). For HA, we determined the presence of inorganic garbage (inogar), organic garbage (orggab) and the distance to roads (disroa). Distance to nearby roads was quantified through the inverse of the distance (m) between plots and the two nearest human roads.

2.2.5. Anthropic disturbance indexes

The indexes of anthropic disturbance (LR, HA and HD; Table 1) were obtained through dimension reduction with a principal component analysis (PCA), following the methods proposed by Martorell and
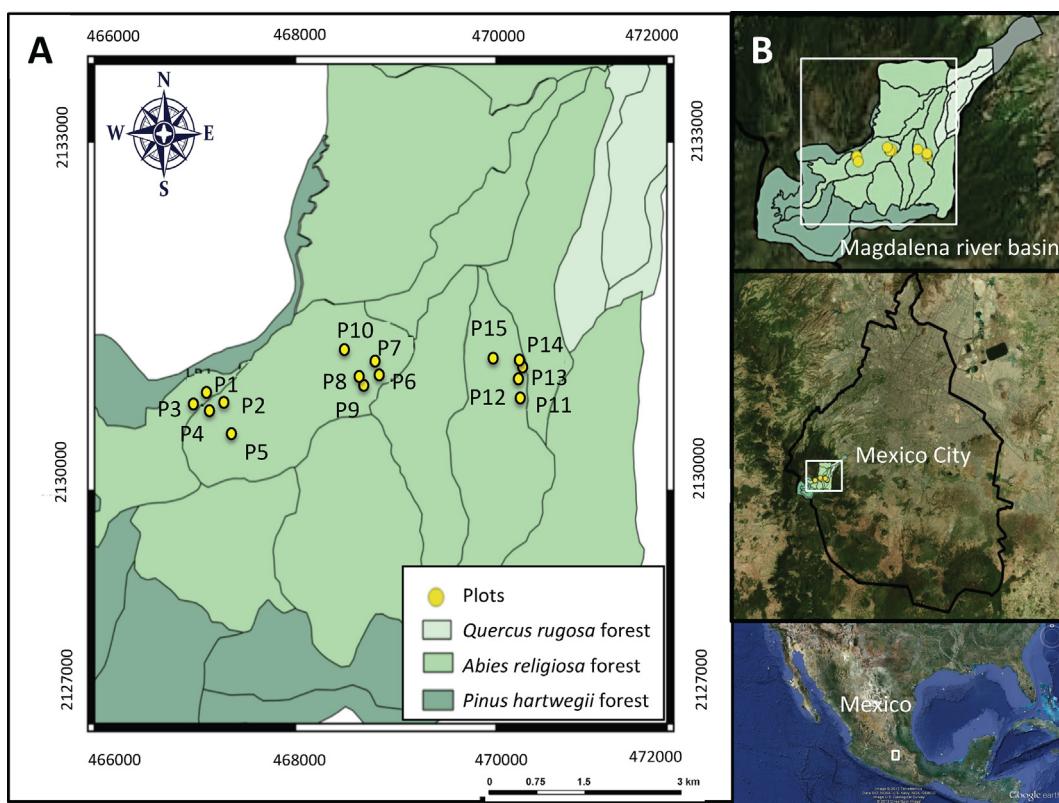
Fig. 3. Study plots (A) in the temperate *Abies religiosa* forest (B) in the Magdalena river basin, Mexico City, Mexico (D). Plots were set at three altitudinal levels (high altitude = 2467–3449 m a.s.l. plots 1–5, intermediate altitude = 3202–3446 m a.s.l., plots 6–10 and low altitude = 3092–3122 m a.s.l., plots 11–15).

Peters (2005) with the statistical software R (v. 3.5.2; R Development Core Team, 2018). From the addition of the scores of every agent in the first component, we obtained the index for each of them. With the addition of the three determined agents we obtained the disturbance index per plot (DI) (Table 1). Therefore, the model that integrates the considered variables to generate the anthropic disturbance index (DI) is the following:

$$DI = -0.036 livdro + 0.540 livroa + 0.275 \times brapla + 0.142 soicom$$
$$+ 0.521 \times weedin + 0.302 \times defore + 0.479 \times canope + 0.008 inogar$$
$$- 0.085 orggar + 0.077 disroa, \tag{2}$$

2.2.6. Environmental variables

In each plot, the environmental variables were quantified in the dry season as well as in the rainy season during the study year (June 2017-June 2018). Temperature was registered continually with hobo data loggers (easy LogUSB-ONSET, Massachusetts, EUA). Light conditions were measured in each plot every two months through hemispheric photographs taken under overcast sky conditions at 8:00 am (digital camera Nikon D80, fisheye lens EX SIGMA4.5 2:28 DCHSM, Tokio, JP) (Table 1). The photographs were analyzed with the Gap Light Analyzer (GLA, 2.0) software to determine the global site factor (GSF), which is defined as the percentage of light (light moles transmitted per unit area) (GLA, 2.0; Frazer et al., 1999).

In both seasons, in each plot, we collected three combined soil samples for chemical analysis. The analyzed variables were pH through the relation of soil and water at 1:2, electric conductivity (EC) in water at a ratio of 1:5, and organic matter (OM) percentage obtained through moist digestion and Walkley-Black determination. The available inorganic phosphorus (P) concentration was determined through the extraction of NaHCO3 0.5 M (pH = 8.5) and colorimetric quantification (Table 1). Nitrogen (N) percentage was obtained through moist digestion with H_2SO_4 Kjeldahl distillation through steam drag and H_2SO_4

(0.05) (Table 1). In addition, three soil samples per plot were collected, weighed, oven dried (105 °C, 48 h) and weighed again to calculate the soil moisture (SM)percentage using the Reynolds (1970) equation:

$$SM = 100(Sf - Sd)/Sd, \tag{3}$$

where *SM* is the percentage of soil moisture, *Sf* is the soil fresh weight and *Sd* is the soil dry weight.

2.2.7. Vegetation sampling and determination of composition indexes

In each plot, we determined the understory species abundances (herbs and shrubs smaller than 3 m in height). For each species, we determined its status: native characteristic species, which are native plants that evolved originally in Mexico and that form part of temperate forests, and native weeds, which are species that evolved originally in Mexico and their establishment is favored by anthropic perturbations (Espinosa and Sarukhán, 1997; Richardson et al. 2000; Calderón de Rzedowski and Rzedowski, 2020; Vibrans, 2015). With the abundances of these two types of species, the indexes of favourable conservation status were determined for each plot, for herbs (FCS.herb) and for shrubs (FCS.shru) (Table 1), using the Helm et al. (2015) equation:

$$FCS = log(abuC/abuW), \tag{4}$$

where *FCS* is the index of favorable conservation status, *abuC* is the abundance of characteristic species and *abuW* is the abundance of native weeds. This index shows the proportion of the abundance of weed species in relation to the abundance of characteristic species.

2.2.8. Leaf attributes and determination of functional metrics

We randomly selected 10 individuals of each species and measured the following metrics for30 leaves of each individual: leaf area (LA; mm^2) with a foliar scanner (Area Meter AM300, ADC, Bio Scientific Ltd, Texas, EUA) and leaf dry matter content (LDMC; mg) through the ratio of the fresh leaf weight /dry leaf weight (oven dried for 48 h, 70 °C).

Table 1

Anthropic disturbance indices description, environmental variables, composition indexes and functional metrics; we present the abbreviations of the names used in the study and the units and scales of measure for the possible values for the variable.

Indicators	Abbreviation	Unit	Scale	Reference
Anthropic disturbance index				
Livestock raising index	LR	NA	$(-\infty, +\infty)$	Martorell & Peters (2005)[a,b]
Habitat deterioration index	HD	NA	$(-\infty, +\infty)$	Martorell and Peters (2005)[a,b]; Caviedes and Ibarra (2017)[a,b]
Human activities index	HA	NA	$(-\infty, +\infty)$	Martorell and Peters (2005)[a,b]
Disturbance index	DI	NA	$(-\infty, +\infty)$	Martorell and Peters (2005)[a,b]
Environmental variables				
Temperature	TEM	°C	−3 a 22	Wolff et al., (2018)[b]
Light	LIG	%	0.5 a 0.60	Théry (2001)[b]
pH	pH	NA	5 a 6.9	Santibáñez-Andrade et al., (2015)[b]
Electrical conductivity	EC	dS/m	0.03 a 0.17	Santibáñez-Andrade et al., (2015)[b]
Organic matter	OM	%	0.11 a 0.39	Santibáñez-Andrade et al., (2015)[b]
Phosphorus (available)	P	ppm	2 a 30	Barton et al., (2016)[b]
Nitrogen	N	%	0.5 a 0.65	Barton et al., (2016)[b]
Soil moisture	SM	%	0. 30 a 0.94	Odriozola et al. (2014)[b]
Composition Index				
Favorable conservation status	FCS	NA	$(-\infty, +\infty)$	Helm et al., (2015)[a,b]
Herbs	FCS.herb			
Shrubs	FCS.shru			
Functional metrics				
Community-weighted mean leaf area	CWM.LA	mm2	$(-\infty, +\infty)$	Violle et al., (2007)[a]; Sitzia et al., (2017)[b]
Characteristic herbs	CWM.LA.herb.C			
Weedy herbs	CWM.LA.herb.W			
Characteristic shrubs	CWM.LA.shru.C			
Weedy shrubs	CWM.LA.shru.W			
Community-weighted mean specific leaf area	CWM.SLA	mm2/mg	$(-\infty, +\infty)$	Violle et al., (2007)[a]; Sitzia et al., (2017)[b]
Herbs characteristic	CWM.SLA.herb.C			
Herbs weed	CWM.SLA.herbW			
Shrubs characteristic	CWM.SLA.shru.C			
Shrubs weed	CWM.SLA.shru.W			
Community-weighted mean leaf dry matter content	CWM.LDMC	mg	$(-\infty, +\infty)$	Violle et al., (2007)[a]; Sitzia et al., (2017)[b]
Herbs characteristic	CWM.LDMC.herb.C			
Herbs weed	CWM.LDMC.herb.W			
Shrubs characteristic	CWM LDMC.shru.C			
Shrubs weed	CWM.LDMC.shru.W			
Functional dispersion	FDis	NA	$(-\infty, +\infty)$	Laliberté and Legendre (2010)[a,b]
Herbs characteristic	FDis.herb.C			
Herbs weed	FDis.herb.W			
Shrubs characteristic	FDis.shru.C			
Shrubs weed	FDis.shru.W			

For the environmental variables, the scale takes into account the minimum and maximum values reported for the study site (Dobler-Morales, 2010; Santibáñez-Andrade et al., 2015; Bonilla-Valencia et al., 2017).

The scale of the functional metrics corresponds to a log transformation.

  [a] Reference that shows its detailed construction.

  [b] Reference that shows its application in the evaluation of perturbations.

Then, the specific leaf area (SLA; mm^2/mg) was obtained for each leaf through the ratio LA/LDMC.

For the four groups of species, characteristic herbs (herb. C), herbaceous weeds (herb. W), characteristic shrubs (shru. C) and shrubby weeds (shru. W), we calculated the community-weighted mean (CWM) for each attribute based on the quantification of the medium dominant value (Table 1) (Violle et al. 2007). With all the attributes determined, the index of functional dispersion (FDis), which reflects the variation in the weighted attributes in terms of the species abundances, was calculated (Table 1) (Laliberté and Legendre, 2010). Low values of FDis indicate the influence of environmental and disturbance filters that promote a high abundance of species with similar attributes (functional convergence), while high FDis values indicate the influence of interactions that promote the complementarity and dissimilarity of attributes (functional divergence) (Hernández-Vargas et al., 2019). These functional metrics were calculated with the attributes and abundance matrices of the species through the FD package (Laliberté and Legendre, 2010) in R software R (v. 3.5.2; R Development Core Team, 2018).

2.2.9. Application of the proposed method of functional indicators in the study system

In the first step of this method, we estimated the effect of the anthropic disturbance agents on the environmental variables (Fig. 2, Step 1), through the possible causal relations documented in the literature. Thus, we evaluated the effect of habitat deterioration (HD) and human activities (HA) on temperature (TEM) and light (LIG) and the effects of HD and livestock raising (LR) on soil moisture content (SM), pH, electric conductivity (EC), organic matter (OM), available phosphorous (P) and nitrogen (N) in the soil (Théry, 2001; Odriozola et al., 2014; Santibáñez-Andrade et al., 2015; Barton et al., 2016; Caviedes and Ibarra, 2017; Wolff et al., 2018). The causal relations were evaluated through LMMs with the lme4 package (Bates et al. 2014) in R software (v. 3.5.2; R Development Core Team, 2018). For the construction of these models, we assumed Gaussian distributions for the environmental variables TEM, pH, EC and P, and for the percentage variables we applied the logit transformation (LIG, OM, N, SM). Models included the random crossed effects of season (dry, rainy) and altitude (three levels). The altitude variation was considered as a random effect in the models, it is a variable that modifies the environment, but it doesn't have a direct relation with disturbance. We estimated the total set of potential models for each environmental variable, and the most plausible models were selected with the smallest AIC.

In the second step, we built the SEMs that evaluated the anthropic effects (exogenous predictors) as well as environmental effects

(endogenous predictors) on the determined functional metrics (CWM. LA, CWM. SLA, CWM. LDMC and FDis; endogenous responses) and the effect of these metrics on the changes on the herb and shrub composition (FCS.her; FCS.shru; exogenous composition responses) (Fig. 2, step 2). The SEMs assumed a Gaussian distribution of the composition indexes (FCS.herb and FCS.shru) and functional metrics (under a log transformation). The inclusion of the LMMs in the construction of the SEMs was not possible due to convergence issues; thus, the SEMs were constructed with LMs, including only fixed effects (anthropic and environmental factors); with variance in the endogenous factors explained by the exogenous factors. For both herbs and shrubs, we selected as functional indictors the functional metrics that showed the smallest AIC.

3. Results

3.1. Anthropic disturbance indexes, of composition, environmental variables and functional metrics

The study plots showed different intensities of anthropic disturbance for the three disturbance agents (LR, Livestock raising HD, Habitat deterioration; and HA, Human activities) as well as for the general index of anthropic disturbance (DI) (Table 2). The disturbance agents with the highest intensity were LR and HD. Disturbance intensity of the three agents and the DI value were different among the three altitudes. Characteristic and weed species, shrub and herbs showed different abundances between plots with different disturbance intensities (Table 2). In Supplementary Material 1, the obtained values of the environmental variables are shown, as well as the index of favorable conservation status (FCS) for herbs (FCS.herb) and shrubs (FCS.shru) and the values of the determined functional metrics (CWM.LA, CWM.SLA, CWM.LDMC and FDis) for the four groups of species (herb.C, herb.W, shru.C and shru.W), with a total of 16 functional metrics for the plant communities.

3.2. Results of the proposed method

3.2.1. Step 1. Anthropic effect on the environment

Table 3; Step 1 show the AIC values of the anthropic effect on the environmental variables. According to the LMMs, only the models associated with phosphorus (P) and pH showed the smallest AIC values than the null model (Table 3; Step 1). For these models, we selected

Table 3
Step 1. Anthropic effect on the environment, **Step 2.** Inference by abduction. LMM = linear mixed model, SEM = structural equations model, ΔAIC = difference in the Akaike's information criterion and K = number of parameters. LR: livestock raising index, HD: habitat deterioration index, P: phosphorus available in soil, pH: pH of soil, CWM.LA: Community-weighted mean leaf area, CWM.SLA: community-weighted mean specific leaf area, CWM.LDMC: community-weighted mean leaf dry matter content, FDis: functional dispersion.

Step 1: Anthropic effect on the environment

Predictor	Environmental response	ΔAIC (K)
LR	P	0 (5)
LR + HD		3.010 (6)
LR*HD		3.130 (7)
Null		7.420 (4)
HD		8.710 (5)
LR*HD	pH	0 (7)
HD		0.710 (5)
Null		2.310 (4)
LR + HD		3.250 (6)
LR		5.080 (5)

Step 2 Inference by abduction

Exogenous predictor	Endogenous predictor	Functional response	ΔAIC (K)
Herbs models			
LR	P	CWM.LA	0 (15)
		CWM.SLA	24.015 (15)
		CWM.LDMC	38.057 (15)
		FDis	6.610(15)
LR*HD	pH	CWM.LA	0 (21)
		CWM.SLA	41.071 (21)
		CWM.LDMC	32.957 (21)
		FDis	21.184 (21)
Shrubs models			
LR	P	CWM.LA	4.670 (15)
		CWM.SLA	18.819 (15)
		CWM.LDMC	50.864 (15)
		FDis	0 (15)
LR*HD	pH	CWM.LA	2.355 (21)
		CWM.SLA	49.399 (21)
		CWM.LDMC	0 (21)
		FDis	9.285 (21)
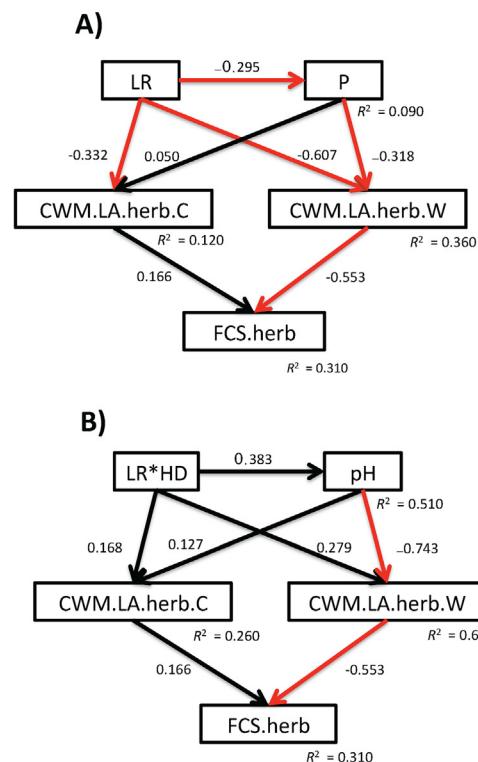
Table 2
Anthropic disturbance indexes and total abundance of characteristic and weed species, herbs and shrubs in the study plot. Study plots are distributed at three altitude levels: (high altitude = 2467–3449 m a.s.l., intermediate level = 3202–3446 m a.s.l., and low altitude = 3092–3122 m a.s.l). C: characteristic species, W: weeds.LR: Livestock raising index, HD: Habitat deterioration index, HA: Human activities index, and DI: general disturbance index obtained from the addition of LR, HA and HD. Negative values indicate low disturbance intensity, positive values indicate higher disturbance intensity.

		Anthropic disturbance index				Abundance			
						Herbs		Shrubs	
Plots	Altitude	LR	HA	HD	DI	C	W	C	W
P1	High	−11,32	0,31	47,02	36,02	83	128	4	187
P2	High	−21,33	3,42	38,7	20,8	102	102	8	213
P3	High	−14,79	−5,52	0,93	−19,38	31	193	12	120
P4	High	5,56	−5,68	22,29	22,18	50	194	27	33
P5	High	−21,81	−3,44	−37,32	−62,57	14	112	61	87
P6	Intermediate	7,76	5,46	−26,2	−12,99	168	243	111	58
P7	Intermediate	49,02	5,34	−18,35	36	160	182	92	76
P8	Intermediate	50,67	0,39	42,11	93,17	232	132	31	55
P9	Intermediate	−4,03	−2,57	18,51	11,9	346	297	96	57
P10	Intermediate	−18,49	0,65	−27,48	−45,33	42	66	140	87
P11	Low	4,98	−0,24	−21,85	−17,11	104	46	111	56
P12	Low	−19,67	−3,56	−36,35	−59,58	61	31	72	113
P13	Low	−11,74	1,41	−2,46	−12,79	81	86	87	84
P14	Low	−16,78	2,19	−40,1	−54,7	131	80	60	94
P15	Low	21,96	1,85	40,56	64,36	81	77	59	88

Step 2: Inference by abduction

Herbs models

Shrubs models
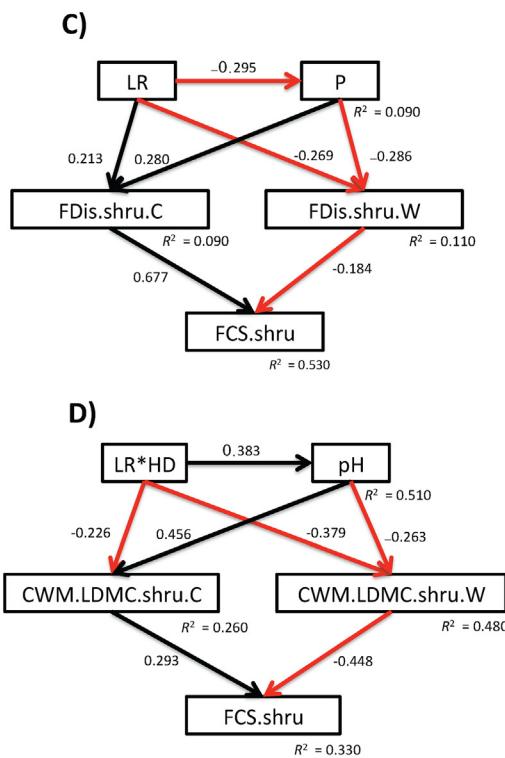
Fig. 4. Structural equation models selected according to the Akaike's information criterion (AIC). Models for herbs (A and B) and for shrubs (C and D). Red arrows represent negative effects, and black arrows represent positive effects. On the arrows, we show the standardized estimated values. The coefficient of determination (R^2) indicates the variance in the endogenous factors explained by the exogenous factors. LR: livestock raising index, HD: habitat deterioration index, P: available phosphorus in soil, pH: pH of soil, CWM.LA: community-weighted mean leaf area, CWM.LDMC: community-weighted mean leaf dry matter content, FDis: functional dispersion. FCS.her: index of favorable conservation status of herbs, FCS.shru: index of favorable conservation status of shrubs. Functional responses of characteristic species (C) and weed (W) species and herbs (herb) and shrubs (shru) species are included.

plausible LMMs with the smallest AIC (ΔAIC = 0; Table 3; Step 1).

3.2.2. Step 2. Abduction by inference

Table 3, Step 2 shows the AIC values of the functional responses. Particularly, for the herb and shrub species, we selected the best- supported SEMs with smallest AIC (ΔAIC = 0; Table 3; Step 2). For the herb species, the best-supported functional indicator was the community-weighted mean for leaf area (CWM. LA), and for shrubs, it was the functional dispersion (FDis) and community-weighted mean of the leaf dry matter content (CWM. LDMC) (Table 3; Step 2). These models show that livestock raising (LR) activities had a negative effect on soil P (Fig. 4; A and C). The interaction of LR with HD (habitat deterioration) showed a positive effect on soil pH (Fig. 4; B and D). Values higher than 0 were discarded because they did not represent the best supported model of the anthropic effect on the functional response.

3.2.3. Herbs models

The best-supported SEMs for herbs showed the negative effects of LR on the functional indicator of characteristic species (CWM.LA.herb.C) and weeds (CWM.LA.herb. W) (Fig. 4, A). The interaction of LR with HD showed positive effects for the functional indicator of characteristic species (CWM.LA.herb.C), as well as for weeds (CWM.LA.herb. W) (Fig. 4, B). In terms of the environmental variables, soil P and pH showed a positive effect on the functional indicators of characteristic species and negative effects on functional indicators of weeds (Fig. 4, A and B). Based on the effect of the functional indicators on composition, we observed positive effects of the functional indicator

of characteristic species on FCS.herb and a negative effect of the functional indicator of weeds on FCS.herb (Fig. 4, A and B).

3.2.4. Shrubs models

The best-supported SEMs for shrub showed positive effects of LR on the functional indicator of characteristic species (FDis.shru. C), and negative effects on the weed indicator (FDis.shru.W) (Fig. 4, C). The interaction between LR and HD showed negative effects on the functional indicators of the characteristic species (CWM.LDMC.shru.C) and weeds (CWM.LDMC.shru.W) (Fig. 4, D). In terms of the environmental factors, soil P and pH showed positive effects on the functional indicators of the characteristic species and negative effects on the functional indicators of weeds (Fig. 4; C and D). Additionally, we found positive effects of the functional indicators of the characteristic species on FCS.shru and negative effects of the weed indicators on FCS.shru (Fig. 4, C and D).

4. Discussion

4.1. Implications of the development of functional indicators

Functional indicators are the key conceptual link to understanding the effect of anthropic activities on composition changes in communities (Tilman et al., 1997; Díaz et al., 2007; Mayfield et al., 2010; Song et al., 2014). Studies such as those by Lavorel and Garnier (2002) and Díaz et al. (2007) have proposed methodological strategies to determine the functional response of plant species, but few studies have

applied such information in the development of functional indicators. To our knowledge, this study is the first to develop functional indicators that simultaneously respond to anthropic disturbance intensity and explain composition changes. Thus, the application of this method represents an excellent opportunity to understand the functional responses of weeds and to understand how their responses increase their establishment under anthropic perturbation conditions. This knowledge will improve predictions of anthropic effects at a functional scale (Funk et al., 2016).

The proposed method presents important theoretical implications. First, even though there is a common understanding in the scientific literature that anthropic disturbance modifies environmental variables, these modifications are rarely considered as change agents in species functional responses (Mayfield et al., 2010; Santibáñez-Andrade et al., 2015; Barton et al., 2016). Second, the anthropic effect on the functional response of species improve the resolution of functional indicators since the effect is quantified through the functional response of the species and not based on the categorization of composition (characteristic species and weeds) (Flynn et al., 2009; Mayfield et al., 2010). Finally, the development of functional indicators based on a causal path allows us to represent more accurately the complexity of the anthropic effect (Santibáñez-Andrade et al., 2015). Thus, it is possible to simultaneously determine the anthropic effect on the functional response of characteristic and weed species.

4.2. Functional indicators of a temperate forest

Over the last decades, the study of leaf attributes has allowed us to determine resource use strategies of species (Castro-Díez et al., 2002; Funk et al., 2017). Often, the success of the weed species under anthropic perturbation conditions has been related to a tendency to efficiently and rapidly acquire resources as represented by high values of leaf area (LA) and specific leaf area (SLA). These attributes allow high rates of nitrogen (N) assimilation during photosynthesis (Feng et al., 2008; Drenovsky et al., 2012). Nevertheless, most of this research has been conducted on herbaceous weeds, and very little is known about shrubby weeds (Funk et al., 2016). The results of this study are consistent with the empirical evidence since the indicator of herbs was the community-weighted mean of leaf area (CWM. LA). Additionally, in this study, we demonstrated that the functional response of shrub species is determined by the leaf dry matter content (CWM.LDMC). This scenario could be because shrub species have a slow life cycle that favors storing and conserving resources through thick leaves with a high content of dry leaf matter (Castro-Díez et al., 2002; Funk et al., 2016).

Under anthropic perturbations, weeds often show a higher variety of different functional responses than characteristic species (for example, a higher leaf and root area, Drenovsky et al., 2012; Ordoñez et al., 2010; Feng et al., 2008). Conversely in this study, livestock raising activities (LR) and habitat deterioration (HD) showed similar negative effects on the functional indicators of characteristic and weed species. This result matches the research reported for other temperate forests, where livestock raising activities and road establishment equally affect the establishment of characteristic and weed species (Ghazoul et al., 2015; Santibáñez-Andrade et al., 2015). However, it is important to note that the interaction of LR and HD had a positive effect on the functional indicators of herbs. This result was probably due to the synergistic effect of both activities in the promotion of vacant areas with a high availability of resources that are quickly used by understory species (Mihók et al., 2005).

At present, anthropic effects on the environment represent one of the main causes of plant diversity loss (Mayfield et al., 2010). In this study, we showed that LR and its interaction with HD promoted a reduction in available P and an increase in soil pH. This situation is most likely due to cation release during the mineralization of cattle manure, which increases soil pH and favors P precipitation in unavailable forms for plants (Dorrough et al., 2006; Trejo-Escareño et al., 2013).

Additionally, the values of soil P and pH were similar to those reported in other disturbed areas of this forest (P; 2 a 30 ppm, pH; 5–6.9; Santibáñez-Andrade et al., 2015). Soil P and pH showed positive effects on the functional indicators of characteristic species, suggesting a tendency to maximize resource acquisition in herb species (higher LA) and to maximize resource conservation in shrub species (higher LDMC) (Feng et al., 2008). In contrast to what was expected, environmental modification of soil P and pH had negative effects on the functional tendencies of weeds. Similarly, several authors, such as Drenovsky et al. (2012), have proposed that the limitation of the leaf functional response of weeds can be compensated by the presence of deeper roots that favor nutrient absorption from soil.

Community assembly after an anthropic disturbance depends on characteristic species that survive as well as on the weeds that colonize the site (Burns, 2006; Mayfield et al., 2010). Thus, communities are integrated by species that are functionally similar, with attributes that allow them to cope with the conditions that are produced by anthropic disturbances (Hernández-Vargas et al., 2019). In this study, LR activities and changes in soil P promoted a decrease in the functional dispersion (FDis) of shrubby weeds. This result suggests a functional convergence effect and the selection of attributes that make species tolerant to perturbation (Richardson et al., 2000; Castro-Díez et al., 2012). However, LR and soil P had positive effects on the FDis of shrub characteristic species. This result suggests an effect of divergence and functional dissimilarity. Authors such as Liu et al. (2016) have demonstrated that the high leaf plasticity of characteristic species in temperate forests can promote a wide range of leaf variation even under perturbation conditions.

Functional attributes directly determine species fitness in a certain environment, which is why they directly contribute to community composition (Mayfield et al., 2010). In this study, we demonstrated in a simultaneous way that leaf functional responses of characteristic species contribute in a positive way with a favorable composition and that weed species contribute in a negative way with a favorable composition. In addition, it is possible that some changes are promoted in the representation of functional attributes due to weed colonization (Feng et al., 2008; Drenovsky et al., 2012; Helm et al., 2015).

4.3. Scope of the inference method by abduction and statistical methods

Authors such as Funk et al. (2017) have noted that the lack of functional indicators is a consequence of the absence of standardized methods capable of handling the complexity of the anthropic effects. Additionally, in different studies, research on functional responses has been an exhaustive and complex search (Niemeijer and de Groot, 2008; Lin et al., 2009). Thus, the main strength of the inference by abduction method is the integrated evaluation of anthropic effects and the practical detection of functional indicators. However, it is important to take into account that the selection of these indicators is based on preselected variables and attributes; thus, its application in future research requires previous knowledge of the study area. Inference by abduction only detects the functional indicators that connect the best causal path of the anthropic effects on composition; therefore, it is possible that other relevant attributes for survival and establishment of the species could remain unidentified.

This study demonstrated that structural equation models (SEMs) represent a good approximation to estimate the causal relations during the development of functional indicators. Similarly, several studies have demonstrated the application of SEM to evaluate causal relations of anthropic effects at the community level (Santibáñez-Andrade et al., 2015; Fan et al., 2016). Specifically, the piecewiseSEM package represents an adequate statistical tool because it allows modelling variables with a distribution different from the Gaussian (through generalized linear models, GLMs; Bolker et al., 2009; Lefcheck, 2016). In addition, this package allows the comparison and selection of models under the Akaike information criterion (AIC), thus avoiding the issues

associated to the use of *P*-values (Burnham and Anderson, 2002). However, depending on the nature of the data, we recommend exploring other statistical tools, such as the Bayesian information criterion, which has also been demonstrated to evaluate successfully functional diversity in hierarchical structures (Funk et al., 2017), and the RLQ analysis, through which it is possible to evaluate causal relationships with categorical data (Dray et al., 2014).

4.4. Final considerations

We suggest applying the proposed method when changes in composition driven by the establishment of weeds are identified, since there are scenarios in which anthropic disturbances do not promote the establishment of weeds. This situation can occur when anthropic disturbances are recent or when they occur at a low intensity, similar to that of some natural disturbances, which allow the recovery of the system (Lin et al., 2009; Daehler, 2003; Niemeijer and de Groot, 2008).

It is important to mention that composition changes can be different among ecosystems. In temperate forests, it has been demonstrated that the anthropic effect on the changes of soil chemical properties promotes a high abundance of weeds (Bonilla-Valencia et al., 2017; Hernández-Vargas et al., 2019). In tropical forests, anthropic effects on light availability seem to affect increases in richness and diversity of weeds (Poorter et al., 2008; Lohbeck et al., 2013). The interpretations of the functional patterns can be different between ecosystems. For example, anthropic activities that cause a loss of soil moisture in temperate forests are the main factors that drive functional convergence (Hernández-Vargas et al., 2019). In dry ecosystems, such as xerophytic shrublands, low moisture regimes cause functional convergence, even in the absence of anthropic perturbation (Poorter et al., 2008; Lohbeck et al., 2013). Therefore, we suggest a rigorous interpretation of the functional indicators based on the study system.

5. Conclusions

The development of functional indicators by the method of inference by abduction allowed us to learn in a simultaneous way the functional responses of the characteristic and weed species under anthropic perturbation conditions. This method represents a methodological advance that will improve the prediction of the anthropic impact at the functional and composition levels. Through the suggested method and with the development of functional indicators, we demonstrated that the anthropic effects on soil P and pH act in different ways in characteristic and weed species in terms of leaf strategies for the acquisition and conservation of resources. The results of this study suggest that the functional responses of weeds are associated with acquisition strategies, while shrubby weeds favor the conservation of resources. This study also showed that the development of functional indicators allows improving our knowledge on the functional responses that promote the establishment of weeds under conditions of anthropic perturbation. This knowledge will allow the prediction of the colonization potential of weeds and their effects at a functional level.

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.ecolind.2020.106515.

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Predictions of the community assemblage in a temperate forest through indicators that evaluate the anthropogenic disturbance effect on natural regeneration

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Predictions of the community assemblage in a temperate forest through indicators that evaluate the anthropogenic disturbance effect on natural regeneration

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ABSTRACT

The causal pathways of the anthropogenic disturbance effect on the above-ground vegetation, seed bank, and seed rain can provide information to understand the dynamic of natural regeneration in order to predict changes in the community assemblage. However, due to the spatial and temporal complexity of the natural regeneration process, these pathways have rarely been tested empirically. Therefore, to understand these pathways on natural regeneration, we propose the integration of composition, richness and functional diversity as indicators of assemblage vulnerability, and apply them to the above-ground vegetation, seed bank, and seed rain. In an *Abies religiosa* forest, in Mexico City, we determined anthropogenic disturbance indicators, environmental indicators and indicators of assemblage vulnerability. In order to assess if anthropogenic disturbances increase the abundance of weeds and modify functional diversity, we built linear mixed models (LMMs), generalized linear mixed models (GLMMs) and structural equation models (SEMs) and selected the best-fitting models according to Akaike's information criterion. We carried out RLQ/Fourth-corner tests in order to determine those regeneration functional traits of weeds that favor their tolerance to anthropogenic disturbances. We found that the anthropogenic disturbances could drive the community into an alternative stable state, in which the presence of weeds could homogenize its functional diversity. Our results showed that the applied indicators reduce the complexity of the study of the natural regeneration process and determine the causal pathways of the anthropogenic disturbance, in order to predict the trends of the community assemblage.

1. Introduction

The increase in anthropogenic activities is a global problem that disrupts the natural regeneration process and threatens the resilience of temperate forests (Ghazoul et al., 2015; Fischer et al., 2016). After a disturbance, the natural regeneration promotes the recovery of the community's assemblage, through the recruitment of new individuals of characteristic species (i.e., native species typical of conserved forests) from the seed rain and the seed bank (Ma et al., 2010; Erfanzadeh et al., 2013; Larson and Funk, 2016; Ma et al., 2019). However, the anthropogenic disturbances such as livestock and deforestation, involve numerous causal pathways at different temporal and spatial scales that negatively affect the natural regeneration of characteristic species and favor seed dispersal, germination, and the establishment of weed species (i.e., arrival of native and introduced weed species, highly competitive under anthropogenic disturbance; ; Gioria and Pyšek, 2016;Martínez-Orea et al., 2020). After lasting and recurring anthropogenic disturbances, weed species could interfere with the formation of the

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community assemblage, producing alternative stable states that are different from the natural historical state (without the input of characteristic species seeds; Westoby et al., 1989; Suding et al., 2004; Cramer et al., 2008; Mayfield et al., 2010; Ma et al., 2019). Consequently, one of the challenges of conservation and management plans is the identifying of causal pathways of anthropogenic effects on natural regeneration that can predict the changes in the community assemblage (Larson and Funk, 2016; Funk et al., 2017).

At present, new methodological strategies are necessary to advance the understanding of the causal pathways of anthropogenic effects on natural regeneration and evaluate its effects on community assemblage. An example can be the metrics of functional diversity (e.g., seed attributes) and metrics that quantify composition changes (e.g., changes in abundances of characteristic and weed species), which recently have been shown to be good indicators to detect the anthropogenic effect on changes in community assemblage in the above-ground vegetation (Mayfield et al., 2010; Helm et al., 2015; Gillison et al., 2019; Bonilla-Valencia et al., 2020). In the seed bank and seed rain the application of these metrics could represent a resource for developing indicators that evaluate the changes of composition and functional diversity, and to predict the vulnerability of the community to develop a different to the original species assemblage, composed mainly by introduced and weed species (Cramer et al., 2008; Larson and Funk, 2016; Funk et al., 2017; Ma et al., 2019).

We define assemblage vulnerability as the loss of the capability of a community to recover their historical natural assemblage through natural regeneration (Ghazoul et al., 2015; Heilpern et al., 2018). From this definition, we propose that community assemblage vulnerability can be evaluated through the integration of three indicators that quantify (1) taxonomic composition changes, promoted by the loss of characteristic species and the increase of weed species abundance, (2) changes in species richness and (3) changes in the functional traits diversity. We hypothesized that low values of the three indicators describe a community with low species richness that is functionally homogeneous and dominated by weeds, and probably with low potential to recover their historical natural assemblage. On the other hand, high values of these indicators describe a community with high richness of characteristic species and with high functional diversity, that has a high potential to recover. These indicators can evaluate simultaneously the functional responses of weed and characteristic species through seed dispersal, seed germination, and their establishment after anthropogenic disturbance (Albrecht and Auerswald, 2009; Drenovsky et al., 2012; Larson and Funk, 2016); and can also help to predict the changes in the community's functional structure (Pakeman and Eastwood, 2013; Larson and Funk, 2016; Bonilla-Valencia et al., 2020).

We developed a method to integratively analyze anthropogenic disturbance and environmental indicators with assemblage vulnerability indicators in the above-ground vegetation, the seed bank, and the seed rain in the *Abies religiosa* (fir) temperate forest in the Magdalena river basin (MRB), Mexico City. The aims of this study were 1) To evaluate the causal pathways of anthropogenic disturbance on natural regeneration, and to predict the trends of the community assemblage, 2) To determine the effects of anthropogenic disturbances on the changes in functional diversity promoted by the presence of weeds, 3) To determine which are the functional traits that favor the abundance of weeds after anthropogenic disturbance. Because the site is under recurrent anthropogenic disturbance, the presence of weed pioneer species that produce large amounts of long-lived seeds is favored. Therefore, we expect (1) a high species similarity between the above-ground vegetation, the soil seed bank, and the seed rain, and (2) low values of the three indicators and functional convergence patterns on the above-ground vegetation, the seed rain, and the seed bank. Likewise, because traits associated with resource acquisition strategy favor the success of weeds, we expected that (3) anthropogenic disturbances would promote the presence of weeds with small seeds, large values of leaf area (LA) and specific leaf area (SLA).

2. Materials and methods

2.1. Study site

The study was carried out in the temperate forest of *Abies religiosa* in the Magdalena river basin (MRB), which is located in the southwest region of the Valley of Mexico (Fig. 1, A and B), between 2900 and 3650 m a.s.l., at coordinates 19° 13′ 53″, 19° 18′ 12″ N and 99° 14′ 50″, 99° 20′ 30′ W. This forest covers 3100 ha. Two vegetation types surround it, a *Quercus* spp. forest at the lowest altitude limit and a *Pinus hartwegii* forest at the highest altitude limit (Castillo-Argüero et al., 2016). According to the Köppen's classification, the *A. religiosa* forest has a temperate sub-humid weather type C (w$_2$) (w) b (i′), with a minimum temperature of 6 °C, a maximum of 20 °C and a mean of 13 °C. Annual precipitation ranges from 950 to 1300 mm (Dobler-Morales, 2010). The rainy season lasts from June to October, while the dry season lasts from November to May (Dobler-Morales, 2010). These forests provide vital ecosystem services to Mexico City population, however, they are constantly affected by anthropogenic disturbances such as deforestation, livestock and weeding. By weeding, we refer to a silvicultural practice that consists in removing the understory vegetation of the forest by the owners, they cut shrubs and herbaceous individuals in order to reduce the competition (Castillo-Argüero et al., 2016).

2.2. Anthropogenic disturbance indicators

During June 2017, we selected 15 plots measuring 30 × 30 m^2 (13, 500 m^2 total) with different degrees of anthropogenic disturbance in the *Abies religiosa* forest of the MRB at three altitude levels (Fig. 1A). In the selection of these areas, we considered the previously published information by Santibáñez-Andrade et al. (2015) and Bonilla-Valencia et al. (2020). In each plot, three indicators of anthropogenic disturbance were determined: (1) livestock activities, (2) habitat deterioration and (3) human activities (as explained below) (Table 1). We worked at both a local scale (inside the 30 × 30 m^2 plots) and at an extended scale that included the area surrounding the plot (60 × 60 m^2).

To determine the livestock indicator (Table 1), we quantified the area (m^2) with the droppings, livestock trails, browsed plants and soil compaction. The quantification of browsed plants was made considering signs of damage in stems and leaf area. Soil compaction was determined by measuring apparent density in three soil samples randomly collected with a cylinder (106.02 cm^3) in each plot. Soil samples were dried in an oven at 105 °C for 24 h and weighed afterwards. Apparent density is the dry soil weight divided by the cylinder volume (g/cm^3; Keller and Håkansson, 2010).

To calculate the habitat deterioration indicator (Table 1), we quantified the area (m^2) that was weeded or deforested, and the size of canopy gaps. Weeding was determined through the evidence of understory vegetation removal and deforestation was determined by the presence of stumps. In each plot, we quantified the canopy openness, through 16 hemispheric photos taken at 8:00 am to avoid light contrasts (digital camera Nikon D80, fisheye lens EX SIGMA4.5 2:28 DCHSM, Tokio, JP). These photos were analyzed with the Gap Light Analyzer (GLA, 2.0) software, which quantifies the fraction of canopy openness. To determine the human activities indicator (Table 1), we quantified the area (m^2) covered by inorganic garbage (such as cans and plastic bottles), organic garbage (plant material product of weeding and deforestation) and the distance to trails, which was quantified through the inverse of the distance (m) between the plots and the two closest roads used by human visitors. We obtained the anthropogenic disturbance indicators by reducing the dimensions using a principal component analysis (PCA) (see details in Bonilla-Valencia et al., 2020) based on a correlation matrix (centering and standardizing data) in the statistical software R (R Development Core Team 2018). The anthropogenic disturbance indicators were determined based on the loadings of the first component (loadings for the first principal component and
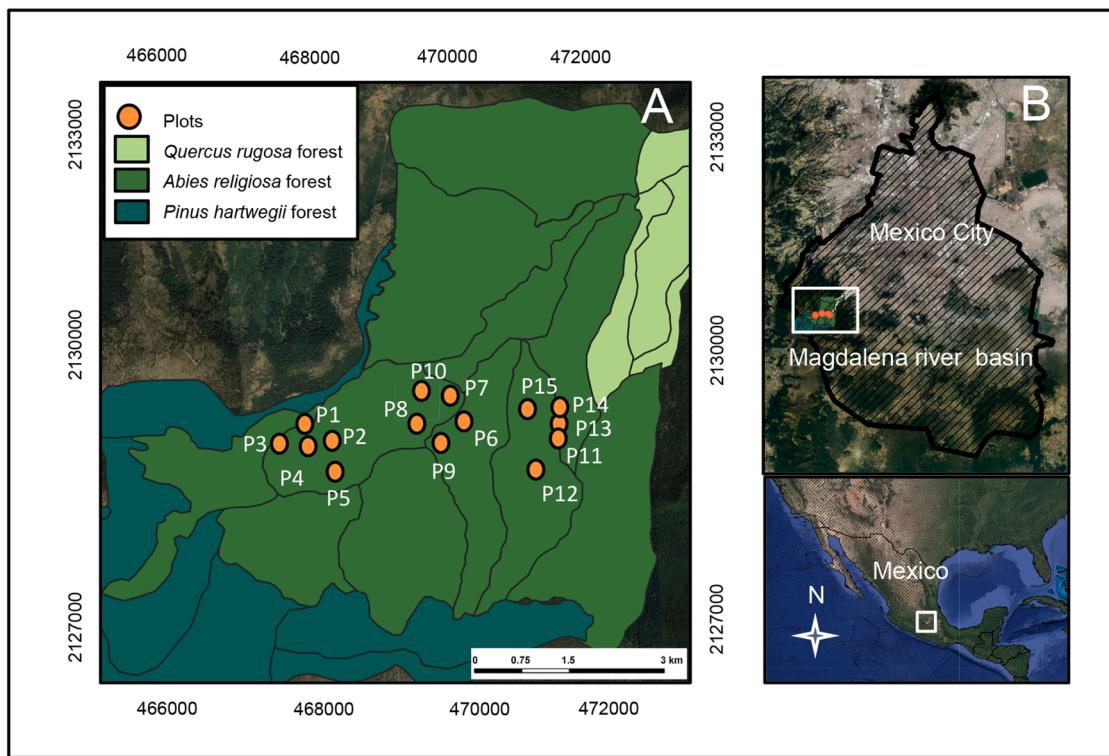
Fig 1. Orange dots represent the study plots in the *Abies religiosa* forest in the Magdalena river basin (A) in Mexico City, Mexico (B). Plots were set at three altitude levels (high = 2467–3449 m a.s.l. plots 1–5; intermediate = 3202–3446 m a.s.l. plots 6–10; and low = 3092–3122 m a.s.l. plots 11–15).

anthropogenic disturbance indicators are shown in the Tables S1 and Table S2).

2.3. Environmental indicators

We quantified environmental variables in each plot, during the rainy and the dry season (Table 1). Temperature was registered using data loggers, which quantified the temperature every two hours (easy LogUSB-ONSET, Massachusetts, USA). The amount of light was quantified through hemispheric photos (as described above) to determine the global site factor, which is defined as the percentage of light mols transmitted through the canopy in an area (Frazer et al., 2000).

For chemical analysis in each season, we randomly collected three mixed samples of soil (200 g) in the first 15 cm topsoil. Analyzed variables were pH, in a water-soil (1:2) mixture (Bates, 1964); electric conductivity, in a water-soil (1:5) mixture (Jackson, 1982); and organic material percentage (OM) through moist digestion (Walkley and Black, 1934) (Table 1). The concentration of inorganic phosphorous (P) was determined through a $NaHCO_3$ 0.5 M (pH = 8.5) extraction with colorimetric determination (Olsen et al., 1954) (Table 1). Nitrogen (N) percentage was obtained through a moist digestion with a solution of H_2SO_4 and Kjeldahl distillation through steam entrainment and titration with H_2SO_4 (Bremner, 1965) (Table 1). Three soil samples per plot were weighed and dried (at 105 °C, for 48 h) to calculate the content of remaining water by difference between the weights of the fresh soil and the dry soil (Reynolds, 1970).

2.4. Assemblage vulnerability indicators

For the above-ground vegetation, seed bank and seed rain components we calculated three assemblage vulnerability indicators. These indicators include (1) species richness, (2) favorable conservation status index (FCS), (3) functional divergence index (FDiv) (Table 1).

2.4.1. Above-ground vegetation, seed rain and seed bank sampling

For a period of one year (June 2017-June 2018) in each plot and for each season (dry and rainy; $n = 90$), we randomly selected three sub-plots (5 × 5 m²) and quantified the abundance of species in the under-story, including trees and shrubs shorter than 2 m. The canopy included trees and shrubs taller than 2 m (quantified at 30 × 30 m²). To quantify the seed rain in each plot and season, we randomly placed three seed rain-collecting traps at the soil level in each season ($n = 90$). The traps were circular (50 cm in diameter and 25 cm in depth) and were composed of metal and cloth mesh. During the study year, every two months, we collected the seeds captured in the traps for their quantification and identification. To evaluate the seed bank in each plot and season, we randomly collected three soil samples (400 g) of 8 cm of surface soil in each season ($n = 90$ plastic trays). These samples were placed in plastic trays (25 × 15 × 6 cm³) and were kept in a greenhouse in the study area (at 2500 m a.s.l. and 17 °C) under saturation watering every week. Every two months, we registered the emerged seedlings; they were subsequently transplanted for taxonomic identification.

2.4.2. Species richness and composition

In each sample of each plot, we determined the species richness and composition (Table 1). For the composition, we used the favorable conservation status index (FCS). The FCS describes the tendency of the community to maintain its original composition as a function of the relationship between the abundance of characteristic species and the abundance of weeds (Helm et al., 2015). Thus, high FCS values indicate a higher representation of characteristic species than weeds and consequently a better conservation status when compared to low FCS values. For this analysis, we considered the following categories of species: 1) *characteristic (CH)*, native plants that conform to the original flora of temperate forests in Mexico; 2) *native weeds (NW)*, pioneer and native species of secondary succession that become established mostly in perturbed areas and have been reported to be dominant at sites under frequent anthropogenic disturbances; and 3) *introduced weeds (IW)*, species with a biogeographic origin and evolutionary history outside of

Table 1

Anthropogenic disturbance, environmental, and assemblage vulnerability indicators description. For environmental indicators the managed scale takes into account the minimum and maximum values reported for the study site (Santibáñez-Andrade et al., 2015; Bonilla-Valencia et al., 2017).

Indicator	Unit	Scale	Reference
Anthropogenic disturbance			
Livestock	NA	(-∞,+∞)	Martorell and Peters (2005)[a,b]
Habitat deterioration	NA	(-∞,+∞)	Bonilla-Valencia et al. (2020)[a,b]
Human activities	NA	(-∞,+∞)	
Environmental			
Temperature	°C	-3 to 22	Santibáñez-Andrade et al. (2015)[b]
Light	%	0.5 to 0.60	Bonilla-Valencia et al., (2020)[a,b]
Soil pH	NA	5 to 6.9	
Soil electric conductivity	dS/m	0.03 to 0.17	
Organic matter	%	0.11 to 0.39	
Phosphorus (available)	ppm	2 to 30	
Nitrogen	%	0.5 to 0.65	
Soil moisture	%	0. 30 to 0.94	
Assemblage vulnerability			
Species richness	NA	(0,+∞)	Mayfield et al. (2010)[a,b]
Favorable conservation status (FCS)	NA	(-∞,+∞)	Helm et al., (2015)[a]
Functional divergence (FDiv)	NA	(0,1)	Bonilla-Valencia et al. (2020)[b] Laliberté and Legendre (2010) Pakeman and Eastwood (2013)[b]

[a] reference that shows its detailed construction,.
[b] reference that shows its application in the evaluation of anthropogenic perturbations.Positive values of the FCS index indicate a higher representation of the characteristic species than weeds species, and negative values of the FCS index indicate a higher representation of the weeds species than characteristic species.When FDiv equals 0, indicate species with similar traits (convergence patterns), and FDiv equals 1 indicate species with different traits (divergent patterns).

Mexico, whose establishment is favored in anthropogenically disturbed areas (for flora and species category; Espinosa-García and Sarukhán, 1997; Richardson et al., 2000; Calderón de Rzedowski and Rzedowski, 2001; Bonilla-Valencia et al., 2017; Vibrans, 2019). The abundances of these three types of species were used to determine the FCS values for each plot with Helm's equation (Helm et al., 2015).

$$FCS = \log(abu\,CH/(abuNW + abuIW)),$$

where *FCS* is the favorable conservation status index, *abu CH* is the characteristic species abundance, *abu NW* is the native weed species abundance and *abu IW* is the abundance of introduced weeds.

2.4.3. Functional traits and functional indicators

For all species, we determined traits that give direct implications for the regeneration process, including life history traits (growth form, life cycle, life form), pollination and dispersal syndromes, reproductive phenology, seed mass, and traits associated to resource use strategies; such as the chlorophyll concentration, leaf area (LA) and specific leaf area (SLA), related to a resource acquisition strategy and leaf dry matter content (LDMC) related to a resource conservative strategy (Table S3; functional explanation and description of the methods for each trait). Considering these traits, in each sample, we calculated the functional divergence (FDiv; Table 1), which is a measure of the diversity of species traits weighted by their abundances, using the FD package (Laliberté and Legendre, 2010) in the R program (R Development Core Team

2018). Due to the presence of quantitative and qualitative traits, we transformed the functional metrics to Gower distances (dissimilarity matrix) through principal coordinate analysis (PCoA) (Gower, 1971). Gower distances standardized each trait between 0 and 1, considering the trait ranges existing in the dataset (Laliberté and Legendre, 2010). Low FDiv values are observed where the disturbance filters promote overlapping of the functional traits of plant species (convergence patterns). High FDiv values are observed where competitive interactions promote the coexistence of species with different traits (divergence patterns) (Hernández-Vargas et al., 2019).

2.5. Statistical analysis

2.5.1. Species similarity between above-ground vegetation, seed rain and seed bank

Through a nonmetric scaling ordination analysis (nMDS), we evaluated the species similarity between the three components of vegetation. The structure of the matrix was built based on the abundance of species using the Bray-Curtis similarity index, we opted for a two-dimensional solution and conducted 100 random iterations. We used the square root transformation on abundance values to avoid biases of the highly abundant species. To calculate the compositional changes between the three components, we carried out a similarity analysis (ANOSIM) with the statistical package vegan (Oksanen et al., 2013) of R software (R Development Core Team 2018). ANOSIM calculated the R statistic from the Bray-Curtis dissimilarity matrix. The R-value varies within an interval of 0–1, where values close to 1 indicate dissimilarity between groups (Oksanen et al., 2013).

2.5.2. Assemblage vulnerability indicators

Differences in assemblage vulnerability index values were evaluated between the above-ground vegetation, seed rain and seed bank. For this analysis, we carried out a Shapiro-Wilk test to determine the normality of the values. ANOVA with Tukey's multiple comparison test was carried out for the FCS (normal distribution), and the Kruskal-Wallis test with multiple comparisons was performed for species richness and FDiv (not normal distribution) in the statistical program R (R Development Core Team 2018).

2.5.3. Causal pathways of the effect of anthropogenic disturbances on the assemblage vulnerability indicators

To evaluate the effects of anthropogenic disturbances and environmental factors on the assemblage vulnerability indicators and depending on the nature of the data, we carried out linear mixed models (LMMs) analyses for FCS (error distribution: Gaussian) and generalized linear mixed models (GLMMs) for species richness (error distribution: Poisson) and FDiv (error distribution: Gamma) with the lme4 (Bates et al., 2014) and glmmTMB packages (Magnusson et al., 2017) in R (R Development Core Team 2018). We evaluated over-dispersal in each model with a Poisson error distribution by the ratio between the residual deviance and the degrees of freedom based on the dispersion test of the statistical package AER to GLM models analyses (Kleiber and Zeileis, 2008). The models included fixed effects (anthropogenic disturbances and environmental factors; predictors variable) and random crossed effects of the plots (season and altitude). In the above-ground vegetation and seed bank models, we considered the anthropogenic and environmental effects at the local scale. In the models of the seed rain, only the effects of anthropogenic disturbances at the extended scale were taken into account as seed rain can be directly affected by anthropogenic disturbances at a major scale, and since there is not a direct relationship between the dispersal of seeds and the studied environmental variables at the local scale (Martínez-Orea et al., 2014). We built the potential models considering the possible additive and interactive relations documented in the literature between the anthropogenic disturbances and environmental variables. Thus, we related the habitat deterioration and human activities with temperature and light. Also, we related

habitat deterioration and livestock with the soil moisture content, pH, electric conductivity, organic matter, available phosphorous and nitrogen (Odrizola et al., 2014; Santibáñez-Andrade et al., 2015; Bonilla--Valencia et al., 2020). The most plausible models were selected according to the Akaike information criterion (ΔAIC) on the basis of (1) a ΔAIC smaller than the null model (without explanatory power) or (2) a ΔAIC smaller than 2 (Burnham and Anderson, 2002). For the obtention of ΔAIC, in Poisson error distribution, we followed the methodology proposed by Mazerolle and Mazerolle (2019). Following the methods developed by Bonilla-Valencia et al. (2020), with the selected models, structural equation models (SEMs) were carried out to integrally evaluate the anthropogenic and environmental effects on the above-ground vegetation, seed rain and seed bank with the statistical package piecewiseSEM (Lefcheck, 2016) in the statistical program R (R Development Core Team 2018).

2.5.4. The relationship between anthropogenic disturbances and environmental factors and species traits

The relationship of the anthropogenic disturbances and environmental variables with the traits of characteristic, native weed and introduced species was evaluated through the RLQ method and the Fourth-corner test in the statistical package ade4 (Dray and Dufour, 2007; Dray et al., 2014) of R software (R Development Core Team 2018). Using this analysis, it was possible to evaluate simultaneously relationships of the different data matrices: R (plot × anthropogenic disturbance indicators/environmental variables), L (plot × species abundance) and Q (species × traits matrix). Following the same logic as for the lineal models, the RLQ analysis of above-ground vegetation and seed bank considered the effects of the anthropogenic disturbance indicators and the environmental variables at the plot level, while the RLQ of the seed rain considered the extended anthropogenic disturbance indicators only. The RLQ analysis considered the phases of the species life cycle, therefore the RLQ analysis of the seed rain and the seed bank; integrated the life history, pollination, dispersal and seed mass traits of the species. Since the species in the above-ground vegetation have already gone through the phase of seeds to their establishment, the above-ground vegetation RLQ analysis integrated all the traits, including those related to the use of resources.

For each RLQ analysis that was carried out, models 2 and 4 suggested by Dray et al. (2014) were evaluated with a significance level (α) of 0.05, using 999 permutations. Model 2 tests the null hypothesis that species are randomly distributed at sites (R is not related to L). Model 4 tests the hypothesis that species are randomly distributed with respect to their traits (L is not related to Q). The two models approach allows a global combined test with separate significance levels, that improves the control of type I error (Dray et al., 2014). In addition, for each RLQ analysis, the Fourth-corner test was carried out to quantify the correlation between the species traits, anthropogenic disturbance and the environmental variables indicators.

3. Results

3.1. Above-ground vegetation, seed rain and seed bank composition

By considering the three components, we identified 99 species (see Appendix), 70 of which belonged to above-ground vegetation, 40 to the seed rain, and 32 to the seed bank. Among the 99 species, 24 were shared between the above-ground vegetation and the seed bank, and 16 were shared between the above-ground vegetation and the seed rain. Only 9 species were present in all three components of vegetation that were evaluated. The species with the highest abundance in the above-ground vegetation was the native weed shrub species *Acaena elongata* (665 individuals); the most abundant species in the seed rain was the characteristic herb species *Brickellia scoparia* (3410 seeds), and the most abundant species in the seed bank was the native weed herb species *Sigesbeckia jorullensis* (568 seedlings). The ANOSIM test showed a high

composition dissimilarity between the seed rain, the above-ground vegetation and the seed bank (R Global=0.7681, $P = 0.001$). These differences in composition were evident in the ordination space of the nonmetric multidimensional scaling analysis (nMDS; Fig. S1). Graphically, we could observe greater separation of the seed rain when compared to the vegetation and the seed bank (Fig. S1).

3.2. Assemblage vulnerability indicators

The assemblage vulnerability indicators showed significant differences between the above-ground vegetation, the seed rain and the seed bank (Fig. 2). FCS was significantly higher in the seed rain and lower in the seed bank ($F = 175.8$, $P < 0.005$, Fig. 2A). The highest values of species richness and FDiv corresponded to the above-ground vegetation, and the lowest values corresponded to the seed rain (Fig. 2B and C; richness; $H = 196.29$, $P < 0.005$, FDiv; $H = 112.13$, $P < 0.005$, Fig. 2B and C).

3.3. Causal pathways of the effect of anthropogenic disturbances on the assemblage vulnerability indicators

For the structural equation models (SEMs), we used the most plausible mixed LMMs and GLMMs to explain the anthropogenic and environmental effects on the assemblage vulnerability indicators ($\Delta AIC < 2.00$) (Table S4, Fig. 3). The SEMs showed that at the local scale, habitat deterioration had a negative effect on the above-ground vegetation assemblage vulnerability indicators (Fig. 3, A, B and C). When habitat deterioration increased, the soil pH became more acid, consequently, higher soil acidity had a positive effect on the assemblage vulnerability indicators of the above-ground vegetation (Fig. 3A, B, and C). For instance, when livestock increases, soil organic matter decreases, both variables had a negative effect on FDiv of above-ground vegetation (Fig. 3C).

Regarding the assemblage vulnerability of the seed bank, light had a negative effect on FCS, and an increase in the soil nitrogen (positively related with habitat deterioration) had a positive effect on species richness and FDiv (Fig. 3, A, B, and C). It should be noted that habitat deterioration at the local scale showed simultaneous and contrasting effects on the FDiv of the above-ground vegetation and the seed bank (Fig. 3C). When the habitat deterioration indicator was high, a decrease in above-ground vegetation FDiv and an increase in seed bank FDiv could be observed, which probably promotes a negative relationship between these two components (Fig. 3C). Our results demonstrate that anthropogenic disturbances at an extended scale modify the seed rain species assemblage. Habitat deterioration had a negative effect on FCS, and positive effects on the species richness and FDiv of the seed rain. Additionally, the increase in livestock had a negative effect on the richness and FDiv of the seed rain (Fig. 3A, B and C).

3.4. Relationship between anthropogenic disturbances and species traits

The RLQ analysis of the above-ground vegetation, seed rain, and seed bank showed an association between the anthropogenic disturbance indices and the environmental variables with the species traits ($P < 0.05$). Only the significant correlations determined through the Fourth-corner analysis were plotted ($P < 0.05$; Fig. 4A, B and C). We demonstrated that at the local scale, the increase in human activities and livestock was positively related to the presence of hemicryptophyte native weeds in the above-ground vegetation (Fig. 4A). Additionally, the increases in habitat deterioration, soil organic matter, and soil nitrogen are related in a positive way to the presence of introduced weeds in the above-ground vegetation (Fig. 4A). The increases in light and temperature are positively related to weeds with a low seed mass and barochorous dispersal syndrome from the seed bank (Fig. 4B).

At an extended scale, anthropogenic disturbance is positively related to the arrival of native weed seeds (Fig. 4C). In contrast, the RLQ
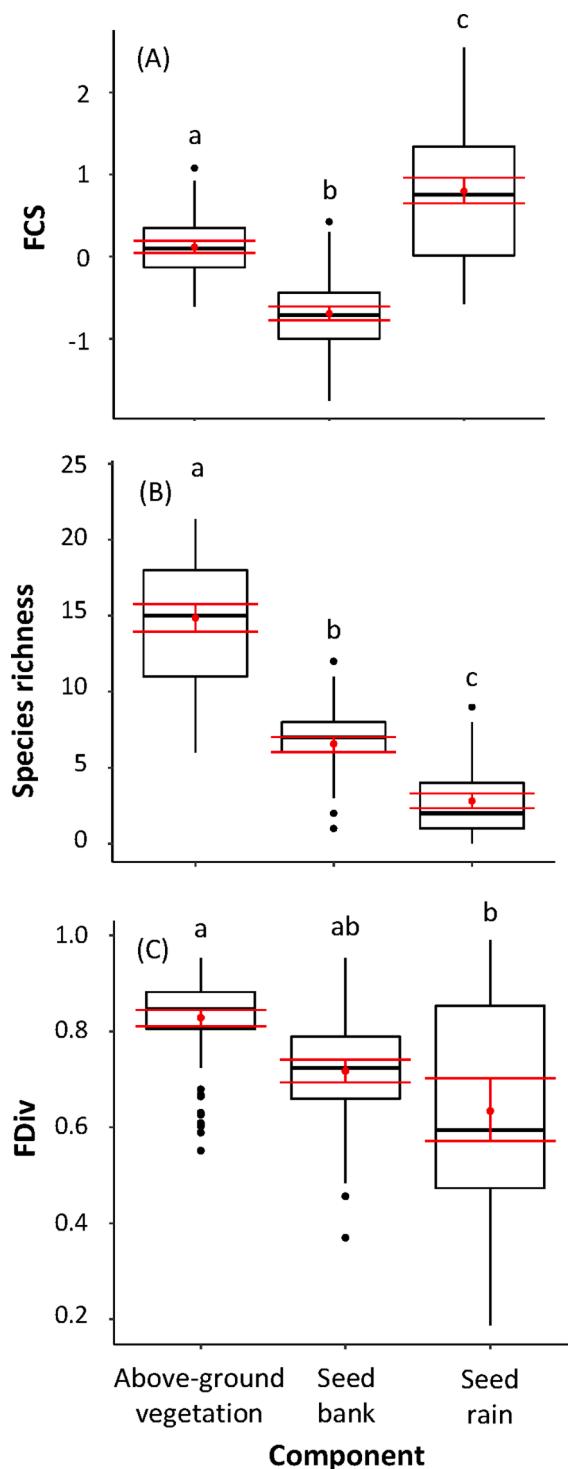
Fig. 2. Boxplots of the assemblage vulnerability indicators. (A) Favorable conservation status index (FCS), (B) species richness and (C), functional divergence (FDiv). The mean values and the confidence intervals (95%) are shown in red, different letters show significant differences ($P < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

analysis showed that the increases in anthropogenic disturbances are negatively related to the presence of characteristic shrub species (some of which can be phanerophytes) with entomophilous pollination (Fig 4. A, B and C). A higher chlorophyll content in the characteristic tree species is positively related to their presence in the above-ground vegetation under high soil pH levels (Fig 4. A). Additionally, the

increases in soil moisture are positively related to the characteristic species in the seed bank (Fig. 4B). Although, the leaf traits (LA and SLA) were not significant in the RLQ analysis; the weeds showed a positive relationship with the herbaceous growth form, which frequently have high values of LA and SLA.

4. Discussion

4.1. Community assemblage stage of the above-ground vegetation, the seed rain and the seed bank

We present the evidence of the causal pathways through which anthropogenic disturbances modify natural regeneration, from the changes in functional diversity promoted by the increase of weeds to the functional attributes that favor their establishment. Understanding the regeneration process is essential to predict the species composition that will potentially develop in the future (Pakeman and Eastwood, 2013). High dissimilarity of species between the above-ground vegetation and the seed bank has often been interpreted as an indicator of a mature state of vegetation without disturbance, and dominated by tree species that form seedling banks or the inclusion of seeds without prolonged dormancy periods (Beauchamp et al., 2013; Martínez-Orea et al., 2020). Although this study demonstrated that the above-ground vegetation and the seed bank presented high compositional dissimilarity, both showed a low FCS (FCS <0). This indicates greater abundance of weed species than characteristic species, probably due to the recurrent disturbance. This is in accordance with the results reported by Albrecht and Auers-wald (2009) and Santibáñez-Andrade et al. (2015), thus demonstrating the dominance of weed species under anthropogenic disturbance. Likewise, the seed bank showed lower values of richness and functional diversity than the above-ground vegetation, possibly caused by the overrepresentation of dormant seeds of pioneer weed species, which usually form persistent seed banks and exhibit traits associated with a ruderal life strategy (Pakeman and Eastwood, 2013; Martínez-Orea et al., 2020). This is why we found a high abundance of herbaceous species such as native weeds *Sigesbeckia jorullensis* and *Geranium seemannii* and introduced species such as *Cardamine hirsuta* and *Plantago major* in the seed bank. While in the above-ground vegetation we found species that conform a greater diversity of life histories traits.

Taking into account the immediate reproductive contribution of species in the above-ground vegetation, we expected high species similarity between the above-ground vegetation and the seed rain. In contrast, the high species dissimilarity between these two components of regeneration revealed the arrival of seeds from other nearby areas. Considering that the seed rain was the component with the highest FCS value, the transport of propagules of characteristic species from other forest areas with better conservation status is likely. In this forest, Martínez-Orea et al. (2014) reported high seed production by characteristic species with anemochorous dispersal, in areas with a low intensity of anthropogenic disturbance. The seed rain showed an overrepresentation of characteristic species of the families Asteraceae and Pinaceae with traits associated to an anemochorous dispersal, such as *Brickellia scoparia*, which produces achenes with feathery appendages, and *Abies religiosa*, with winged seeds.

Although, the seed rain represents an important pool for the recruitment of individuals of characteristic species, through which forest recuperation could occur; it is important to consider the germination of these species. In temperate forests, many characteristic species exhibit morphophysiological dormant seeds that require specific environmental conditions to germinate (e.g., alternation between warm and cold temperatures; Ma et al., 2010; Martínez-Orea et al., 2020). Therefore, anthropogenic disturbance can negatively affect the germination of some characteristic species. For example, in this study, the characteristic species *Symphoricarpos microphyllus* (with morphophysiological seed dormancy, Martínez-Orea et al., 2019), present in the seed rain is not abundant in the above-ground vegetation and, was not found in the seed
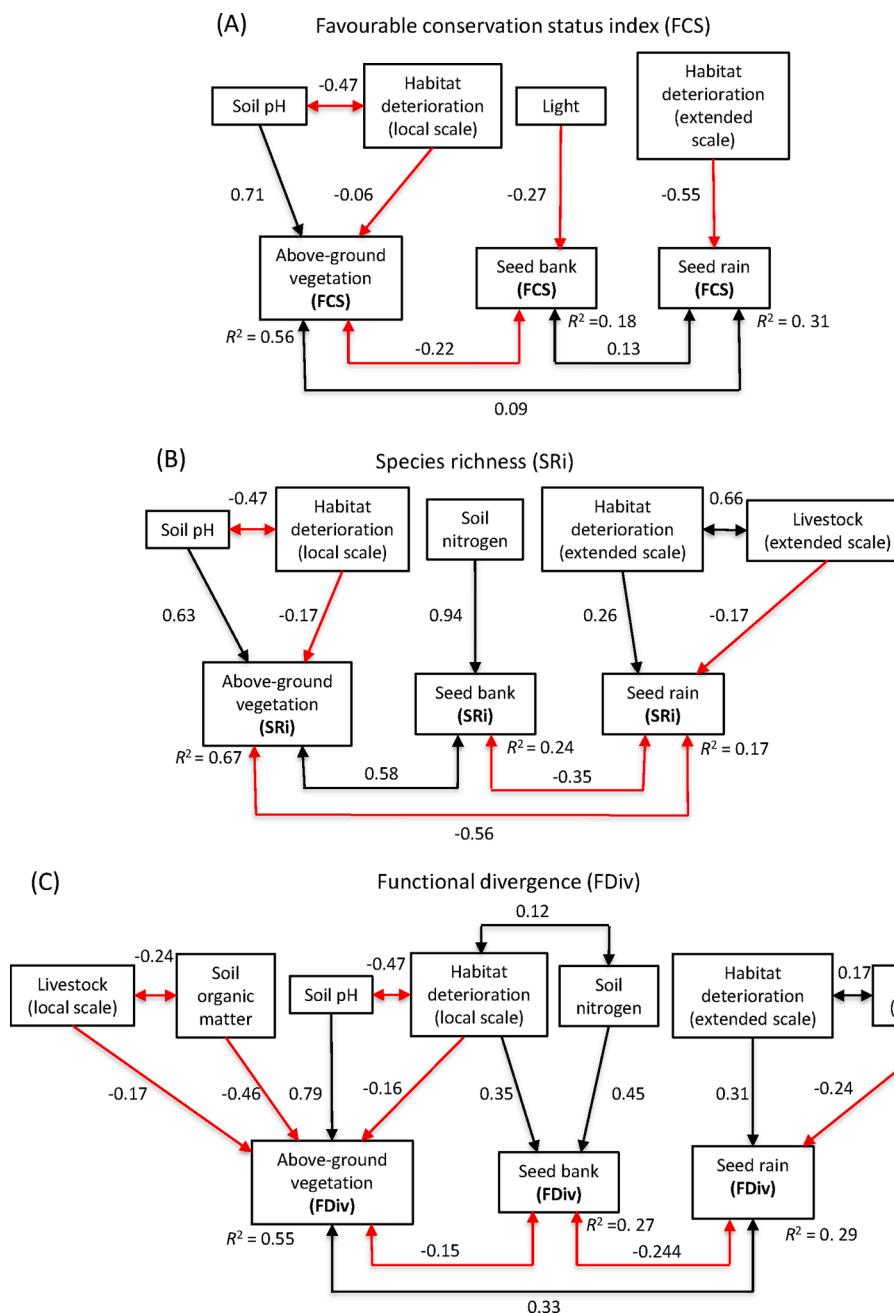
Fig. 3. Structural equation models (SEMs) of the anthropogenic disturbance effect on the community assemblage vulnerability indexes, (A) SEM of the favorable conservation status index (FCS), (B) SEM of species richness (SRi), (C) SEM of functional divergence (FDiv). Red arrows represent negative effects, and black arrows represent positive effects. On the unidirectional arrows, the standardized estimator values are shown. On the bidirectional arrows, the standardized covariation estimators are shown. R^2 indicates the variation of endogenous factors explained by the exogenous factors.

bank.

4.2. Causal pathways of the effects of anthropogenic disturbance on assemblage vulnerability indicators

The SEM analysis showed the causal pathways of the effects of anthropogenic disturbances on natural regeneration and their effect on the community assemblage through an increased abundance of weed species. At the local scale, the simultaneous and contrasting effects of habitat deterioration on the seed bank and the above-ground vegetation showed feedback effects in the system. In the first instance, habitat deterioration is related with an increase of FDiv of the seed bank, particularly of weed species, which can persist in the seed bank (Gioria and Pyšek, 2016).

Specifically, light reduced FCS (i.e., favoring the presence of weed species), while an increased availability of soil nitrogen promoted an increase in species richness and FDiv. This tendency has already been

reported in other studies, which have demonstrated that increases in the availability of resources favor the coexistence of functionally different species (Hernández-Vargas et al., 2019; Fried et al., 2019; Ma et al., 2019). Our results were probably due to habitat deterioration such as deforestation favoring an increased light at the soil surface and promoting the germination of weed quiescent or dormant seeds (Ma et al., 2010; Gioria and Pyšek, 2016). Likewise, the deforestation and deposition of plant material (by weeding) as well as livestock could be related to an increase in soil nitrogen and the seed germination of some species (Schneider and Allen, 2012).

Contrary to what is observed in the seed bank, we obtained evidence that anthropogenic activities promote the presence of functionally similar weeds in the above-ground vegetation. Specifically, we found that habitat deterioration has a negative effect on FCS (i.e., favors the presence of weed species) and on species richness in the above-ground vegetation. Likewise, habitat deterioration, livestock, and the loss of soil organic matter have a negative effect on the above-ground

(A) Above-ground vegetation

(B) Seed bank

(C) Seed rain
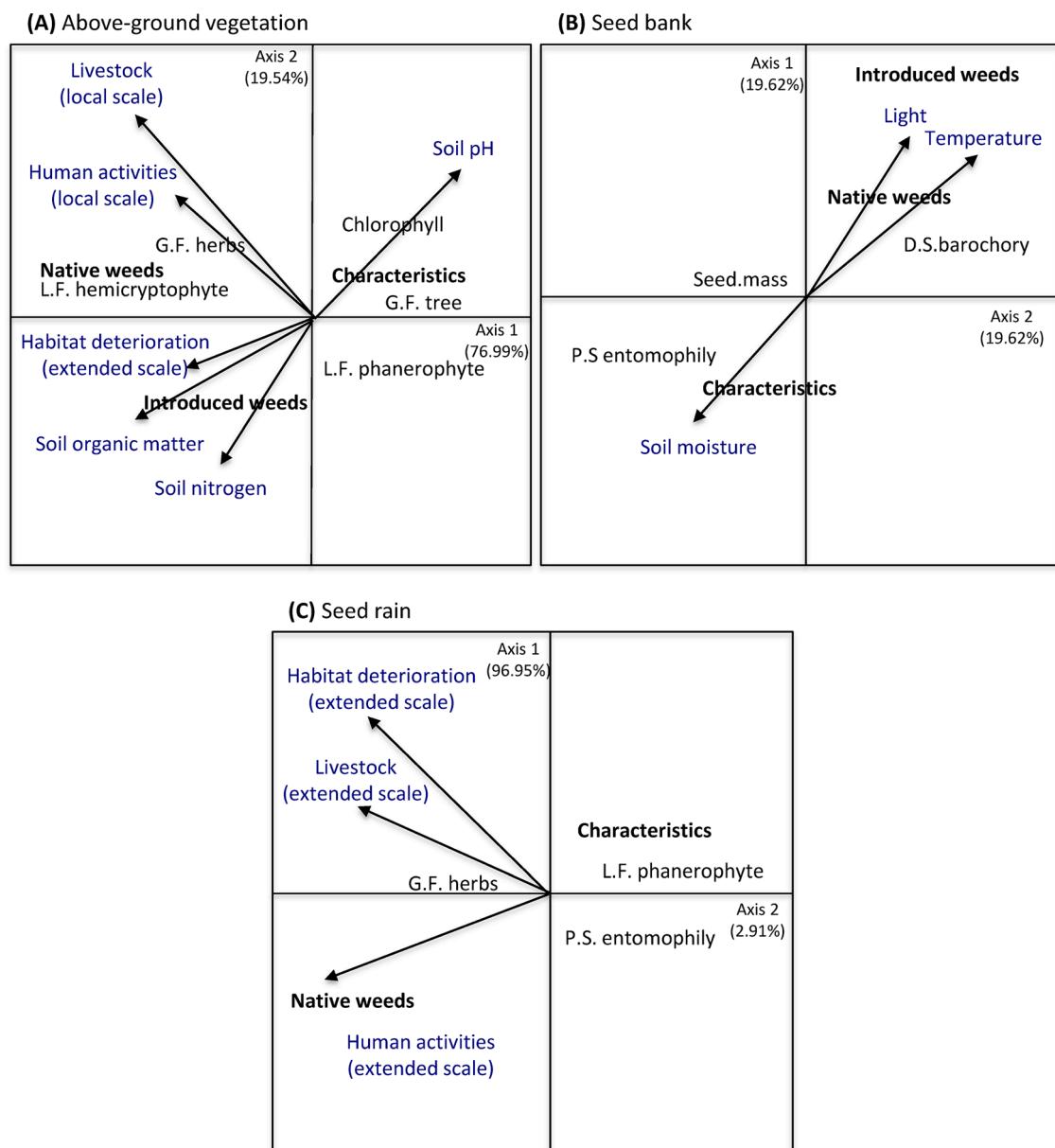
Fig. 4. RLQ diagrams ($d = 2$) defined by the first two that show the relationship between anthropogenic disturbances and the environmental variables with the characteristic, native and introduced weed species traits Only the significant relationships determined by the Fourth-corner test are shown ($P < 0.05$): G.F. =growth form, L.F. =Life form, P.S.= pollination syndrome, D.S. =dispersal syndrome. (A) RLQ of the above-ground vegetation, (B) RLQ of the seed bank and (C) RLQ of the seed rain.

vegetation FDiv. These findings demonstrated that anthropogenic disturbance and environmental changes generate a functional convergence effect on the community assemblage (Pakeman and Eastwood, 2013; Fried et al., 2019). In this scenario, anthropogenic disturbances would function as filters that favor the establishment of weeds sharing similar traits tolerant to anthropogenic perturbations (i.e., small seeds and large values of leaf area); therefore, likely, characteristic species that are less competitive will be excluded (Mayfield et al., 2010; Fried et al., 2019).

Our results also indicate that the arrival of some species through the seed rain can maintain the feedback effects during the establishment of weeds. According to the SEM analysis, at an extended scale, habitat deterioration favors the dispersal of weed seeds with a high diversity of functional traits. Most likely, deforestation and weeding can reduce obstacles to the seed dispersal of some weeds by reducing plant cover (which can act as a physical barrier). However, livestock promoted a

pattern of functional convergence in the seed rain. Although the effect of livestock on seed rain has not been widely documented, Marteinsdóttir (2014); Tjelele et al., (2015) and de Moraes-Stefanello et al. (2019), have demonstrated that the presence of cattle can severely restrict seed dispersal by the consumption of the seeds of some species by the animals. In this scenario, the community is susceptible to fall or stay in an alternative steady state, with a species composition that is completely different from the original historical vegetation state (Suding et al., 2004; (Ghazoul et al., 2015); Ma et al., 2019). Therefore, our results show that the recruitment of weed species with similar traits will be promoted in the long term, and the system will probably remain functionally homogeneous in an alternative stable state and will continue to show a low resilience capability.

4.3. Relationship between anthropogenic disturbances and weed species traits

Identifying which traits of weed species have persisted and which have been displaced can help elucidate species assemblage mechanisms during natural regeneration (Larson and Funk, 2016). In this study, the application of the RLQ method and Fourth-corner analysis identified the traits that favor weed recruitment in areas of high anthropogenic disturbance. As the intensity of anthropogenic disturbances increase, the seed rain and above-ground vegetation contain a higher abundance of herbaceous weeds (including some hemicryptophytes); characterized by the production of high quantities of small seeds whose dispersal is favored by wind (Erfanzadeh et al., 2013; Martínez-Orea et al., 2014), and by high growth rates in conditions of high availability of resources (Funk et al., 2016; Dyderski and Jagodziński, 2019). Although the traits (LA and SLA) associated with a resource acquisition strategy (Hernández-Vargas et al., 2019; Funk et al., 2016) did not significantly respond to the disturbance, the introduced weeds showed this tendency. The positive relationship between introduced weeds with the habitat deterioration and the quality of the organic matter that is incorporated into the soil probably indicates higher leaf production, showing higher values of LA and SLA. Wang et al., (2017) demonstrated that introduced weed species generally show high LA and SLA values that increase the decomposition rate and soil organic matter with allelopathic effects on some characteristic species.

Our study also proved that open canopy areas that are characterized by more light and higher temperatures (probably more disturbed) can favor the germination of small weed seeds. Small seeds are a trait of pioneer species that is generally related to the production of seeds with low reserve contents and therefore high dependence on increased light during germination (Milberg et al., 2000) Other traits such as the presence of dormancy in the seeds of weed species possibly favor their persistence during long spans of time and enable their germination when the conditions become favorable (Pakeman and Eastwood, 2013; Martínez-Orea et al., 2020). We found evidence that those weed species that form seed banks have a high proportion of barochorous seeds. Authors such as Ramos et al., (2017) have demonstrated that dormancy is a trait that could help in preventing the germination of seeds that simultaneously fall near the mother plant and decrease intra- or interspecific competition.

4.4. Relationship between anthropogenic disturbances and characteristics species traits

The RLQ analysis demonstrated that the presence of the characteristic species was favored in conditions of high soil moisture, frequently in areas without deforestation and without weeding, which matches the results reported by Santibáñez-Andrade et al., (2015) and Bonilla-Valencia et al., (2017). The RLQ test also revealed that increased soil pH values are related to an increase in chlorophyll values of characteristic species. This is probably because soil pH values (5.2–6.4 pH) are lower than the values that are frequently required to promote a high availability of soil nutrients (7.0 pH; Härdtle et al., 2004). Therefore, restoration activities may be necessary to promote soil pH conditions required for the germination and/or establishment of characteristic species. In addition, the negative relationship of anthropogenic disturbance with characteristic species with entomophilic pollination suggests a limitation of biotic pollination agents. As has been observed in other temperate ecosystems, anthropogenic perturbations act as a filter that restricts the movement of pollinators and thereby inhibits the sexual reproduction of characteristic species (Girão et al., 2007). Over time, this can reduce the seed dispersal of characteristic species and the resilience capability of the forest (Jesus et al., 2012). In future studies, it will be necessary to evaluate whether clonal propagation could compensate for the negative effects of anthropogenic disturbances on sexual reproduction in characteristic species (as seen in Latzel et al.,

2008).

4.5. Final consideration of the assemblage vulnerability indicators

To our knowledge, this study is the first one to develop functional indicators of natural regeneration that simultaneously respond to the anthropogenic disturbance intensity and predict changes in the community assemblage. Therefore, these indicators can be a tool for the development of ecological restoration and conservation strategies. However, it is essential to consider that the indicators can point to different possible outcomes. For example, different scenarios could occur, wherein the arrival of introduced weeds with traits different from those present in the occurring species could increase the functional diversity (i.e., functional divergence) (Mayfield et al., 2010; Fried et al., 2019). Likewise, the applicability of these indicators may differ among ecosystems. For example, in tropical forests, a large fraction of the characteristic species exhibits transient seed banks; therefore, the low species richness in the seed banks may be an independent state from anthropogenic disturbance (Lohbeck et al., 2013; Hernandez-Vargas et al., 2019). In dry ecosystems, the dry season seems to be the most restrictive factor for the dispersal of many anemochorous species; as well as, the low moisture regimes can cause functional convergence, even in the absence of anthropogenic perturbation (Lohbeck et al., 2013).

5. Conclusions

The application of assemblage vulnerability indicators represents a methodological advance to predict changes in community assemblage promoted by the presence of weeds, based on which ecological restoration and management plans can be developed. In this study, the application of these indicators allowed us to increase our knowledge on the conservation status and to make predictions on the possible directions of the species assemblage in the *Abies religiosa* forest of the MRB. Despite the movement of characteristic species into the study site through seed dispersal, our results showed that the native and introduced weeds dominate in the above-ground vegetation and the seed bank. Thus, we predict that the vegetation will become functionally homogeneous. Under this scenario, the regeneration of several characteristic species will be probably inhibited, and the trajectory of vegetation can be directed to an alternative stable state, in which intensive ecological restoration activities will be needed.

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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2021.151764.

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Table S1. Measure loadings for the first principal component in the anthropic disturbance index at local and extended scale. Variance explained for the first principal component; 31% at local scale and 57% at extended scale.

Indicator	Activities	PC1 (local scale)	PC1 (extended scale)
Livestock	Droppings	-0.036	0.065
	Livestock trails	0.54	0.363
	Browsed plants	0.275	0.228
	Soil compaction	0.142	0.478
Habitat deterioration	Weeded	0.521	0.355
	Deforestation	0.302	0.322
	Canopy gaps	0.479	0.322
Human activities	Inorganic garbage	0.08	0.587
	Organic garbage	-0.085	0.046
	Distance to trails	0.077	0.076

Table S2. Anthropic disturbance indicators; livestock, habitat deterioration and human activities (at local scale and at extended scale).

	Local scale			Extended scale		
Plot	Livestock	Habitat deterioration	Human activities	Livestock	Habitat deterioration	Human activities
P1	-11.316	47.020	0.312	19.525	14.894	21.284
P2	-21.326	38.704	3.421	25.225	24.432	20.236
P3	-14.788	0.933	-5.522	-7.295	15.033	-7.657
P4	5.564	22.292	-5.675	6.382	-6.666	-10.453
P5	-21.809	-37.320	-3.438	36.509	5.091	21.561
P6	7.761	-26.205	5.457	7.209	6.592	10.256
P7	49.021	-18.353	5.336	-3.84	-15.032	26.201
P8	50.673	42.108	0.389	3.666	1.085	0.030
P9	-4.034	18.507	-2.572	2.469	1.801	-9.101
P10	-18.489	-27.483	0.645	-14.469	-11.773	-16.271
P11	4.983	-21.852	-0.240	-16.032	-5.581	-6.091
P12	-19.674	-36.348	-3.556	-19.621	-8.214	-15.114
P13	-11.743	-2.460	1.412	-11.521	-12.227	-11.876
P14	-16.781	-40.100	2.186	-23.4	-8.081	-17.252
P15	21.959	40.557	1.846	-4.803	-1.353	-5.752

Description of the methods for each trait

The determination of the life history traits of pollination and dispersal syndromes (Table S3) was based on field and herbarium observations, and the descriptions of van der Pijl (1982), Calderón de Rzedowski and Rzedowski (2001), Martínez-Orea et al. (2012), and Castillo-Argüero et al. (2016). In addition, for each species, we determined the flowering and fructification patterns (Table S3) through field observations during the study by the presence of flowers and/or fruits in the species, having three phenological categories; dry (November to April), rainy (May to October) and continuous pattern (all year long). The phenology of the species that did not show flowering or fruiting was determined based on Bonilla-Valencia et al. (2017). Seed mass was determined by consulting the seed databases of the Royal Botanic Garden Kew (2019) (Table S3). To evaluate the traits associated with the use of resources (Table S3), we randomly selected 10 individuals for each species. In each individual, we randomly chose 30 mature leaves. We calculated the leaf area (LA; mm^2) using a foliar scanner (Area Meter AM300, ADC, Bio Scientific Ltd, Texas, USA), the leaf dry matter content (LDMC; mg) as the ratio of the fresh leaf weight to the dry leaf weight (oven dried at 70 °C for 48 h) and the specific leaf area (SLA; mm^2/mg) as the ratio of LA and LDMC. These traits were selected considering the fact that high LA and SLA values are associated with a large leaf lamina, a high photosynthetic rate, and a resource acquisition strategy. High LDMC values are associated with a thicker leaf lamina and a resource conservative strategy (Hernández-Vargas et al., 2019). In addition, we recorded chlorophyll concentration (Table S3) at five spots on each leaf (four at the edge and one in the center) with an Opti Sciences (CL; mg/mm^2) device.

Table S3. Traits associated with natural regeneration; life history, pollination, dispersal, germination and resource use strategies. References show the importance of each group of traits in natural regeneration. QL = qualitative traits, QN = quantitative traits.

	Type	Trait	Explication	Reference
Life histories				
Biogeographic origin status	QL	characteristic (CH) native weed (NW) introduced weed (IW)	Traits that influence the establishment and permanence of individuals.	Espinosa-Garcia and Sarukhán (1997) Richardson et al (2000) Drenovsky et al. (2012) Funk et al. (2016)
Growth form	QL	herbs shrubs tree		
Life cycle	QL	annual perennial		
Life form	QL	chamaephyte cryptophyte hemicryptophyte phanerophyte therophyte		
Pollination/Dispersal				
Pollination syndromes (PS)	QL	anemophily entomophily mixed ornithophily	Traits associated that influence the reproductive success of species.	Girão et al. (2007) Pakeman and Eastwood (2013) Larson and Funk (2016) Bonilla-Valencia et al. (2017)
Flower phenology	QL	continuous dry rainy		
Dispersal syndromes	QL	anemochory barochory zoochory		
Fruit phenology	QN	continuous dry rainy		
Dispersal/ Germination				
Seed mass	QN	mg	Seed mass is related to seed dispersal and to the reserves content.	Pakeman and Eastwood (2013) Larson and Funk (2016)

Table S3. *Continues*

	Type	Trait	Explication	Reference
Resource use				
Leaf area (LA)	QN	mm2	Traits that influence the use of resources. High LA and SLA values show a resource acquisition strategy.	Larson and Funk (2016) Funk et al. (2016) Hernández-Vargas et al. (2019)
Specific leaf area (SLA)	QN	mm^2/mg		
Leaf dry matter content (LDMC)	QN	mg	High values LDMC show a conservative resources strategy.	
Chlorophyll	QN	mg/mm^2		

Table S4. Most plausible linear mixed model (LMMs) and generalized linear mixed models (GLMMs) explaining the anthropic and environmental effects on the assemblag*e* vulnerability indicators (ΔAIC <2.00). ΔAIC = difference in relative Akaike information weight, K = number of parameters.

| Anthropic disturbance and environmental indicators (Predictor)	Assemblage vulnerability indicators (Response)	ΔAIC (K)
	Favorable conservation status (FCS)	
Soil pH	Above-ground vegetation	0(4)
Habitat deterioration (local scale) + Soil pH		0.55(5)
Light	Seed bank	0(4)
Habitat deterioration (extended scale)	Seed rain	0(3)
	Species richness	
Soil pH	Above-ground vegetation	0(3)
Habitat deterioration (local scale) + Soil pH		1.47(4)
Soil nitrogen	Seed bank	0(3)
Habitat deterioration (extended scale) * Livestock (extended scale)	Seed rain	0(4)
	Functional divergence (FDiv)	
Soil pH	Above-ground vegetation	0(3)
Livestock (local scale) * Soil organic matter		0.04(5)
Habitat deterioration (local scale) * Soil pH		0.11(5)
Soil nitrogen	Seed bank	0(3)
Habitat deterioration (local scale) * Soil nitrogen		1.23(5)
Habitat deterioration (extended scale) + Livestock (extended scale)	Seed rain	0(4)
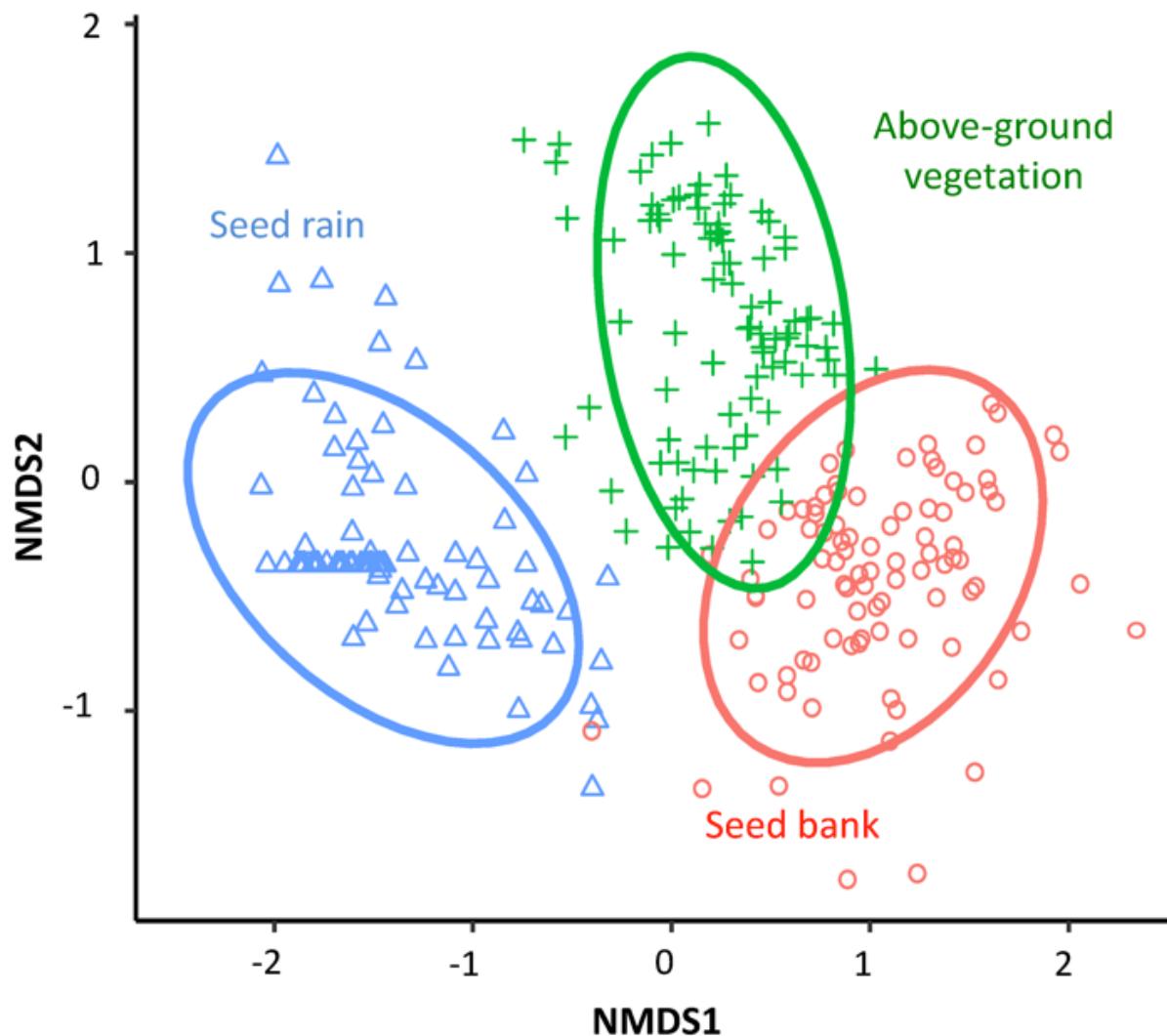
Fig. S1. Nonmetric multidimensional scaling analysis (nMDS) between the established components of vegetation. Stress =0.1730. Green crosses = above-ground vegetation, red circles = seed bank, blue triangles = seed rain.

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DISCUSIÓN GENERAL

Evaluación de la integridad funcional del bosque de *Abies religiosa* de la CRM

DISCUSIÓN GENERAL

EVALUACIÓN DE LA INTEGRIDAD FUNCIONAL DEL BOSQUE DE *ABIES RELIGIOSA* DE LA CRM

La integridad ecológica es definida como una medida de la composición, estructura y función de un ecosistema en relación con el rango de variación natural o histórico del sistema (Parrish *et al.,* 2003; Tierney *et al.,* 2009). La integridad ecológica es un termino que considera diferentes aspectos como, (1) la integridad funcional y estructural del ecosistema, (2) la estabilidad y resiliencia del ecosistema, (3) la integridad de la vida silvestre y (3) la integridad de la calidad y valor de los ecosistemas para la provisión de bienes y servicios (Woodley, 2010; Roche y Campagne*,* 2017). Dentro del estudio de la integridad ecológica uno de los mayores retos es poder conocer la capacidad de resiliencia de los ecosistemas para mantener su integridad funcional después de un evento de disturbio antropogénico (Andresen *et al.,* 2001; Ghazoul *et al.,* 2015; Brown-Williams *et al.,* 2016). Al respecto Angelar y García (2005) y Ma et al. (2021) mencionan que una forma de estimar el cambio de la integridad funcional después de un evento de disturbio es a través de la composición característica presente en las fuentes de regeneración en las comunidades (e.g., banco y lluvia de semillas). Después de un evento de disturbio, una comunidad con una alta dominancia de especies característica es un indicador de resiliencia, que demuestra la contribución de estas especies en el mantenimiento de los procesos ecológicos originales a través del tiempo (Parrish *et al.,* 2003; Woodley, 2010; Ghazoul *et al.,* 2015). Por el contrario, cuando las perturbaciones antropogénicas eliminan a las especies características en las fuentes de regeneración y se favorece la entrada de especies malezas las comunidades tienden a generar cambios drásticos en los procesos ecológicos (Drenovsky *et al.,* 2012a; Pakeman *et al.,* 2013; Ghazoul *et al.,* 2015). Considerando lo anterior, es evidente la necesidad de desarrollar indicadores ecológicos que aíslen y examinen las respuestas funcionales de las especies de malezas y características a factores de perturbación antropogénica (Violle *et al.,* 2007; Niemeijer y Groot, 2008; Müller *et al.,* 2012). Sin embargo, hasta el momento presente durante la elaboración de esta tesis, el método de *"inferencia Lógica por abducción"* es el único método que considera durante la construcción de indicadores, que la respuesta funcional de las especies características y de las malezas es diferente ante los incrementos de disturbio

antropogénico (Capítulo 3). Método a través del cual fue posible hacer una evaluación del efecto de las actividades antropogénicas sobre la integridad funcional del bosque de *A. religiosa* (Capítulo 4).

Al igual que en el bosque de *A. religiosa,* en la mayoría de los ecosistemas las actividades antropogénicas modifican diferentes variables ambientales, como la temperatura, la luz y las propiedades químicas del suelo (Odrizola *et al.,* 2014; Théry *et al.,* 2001; Barton *et al.,* 2016; Wolff *et al.,* 2018). Sin embargo, los efectos de las modificaciones ambientales pocas veces han sido incorporados en la construcción de indicadores ecológicos. En el bosque templado de *Abies religiosa* de la CRM, el desarrollo del método de *"Inferencia Lógica por Abducción"* demostró ser una herramienta eficiente para determinar cuales son las variables ambientales que son modificadas por las actividades antropogénicas. En este estudio se demostró que las actividades de ganadería (AG) y las actividades de deterioro del hábitat (DH) son los principales promotores de los cambios ambientales y de diversidad funcional, mientras que las actividades humanas (AH) no tuvieron ningún efecto significativo. Probablemente esto sucede porque las actividades humanas, como la presencia de basura no tienen un efecto directo sobre la modificación ambiental (Santibáñez-Andrade *et al.,* 2015). Particularmente el efecto negativo de las actividades ganaderas sobre el fósforo inorgánico (P) en el suelo (ortofosfato asimilable para las plantas) demostró ser uno de principales indicadores ambientales que modifica la diversidad funcional en el bosque de *A. religiosa*. Se ha demostrado que a mayor compactación del suelo generalmente promueve una mayor densidad aparente y ruptura de agregados que incrementan la pérdida de fósforo por erosión y lixiviación (Barzegar *et al.,* 2006; Sadeh-Zadeh *et al.,* 2008; Zemke *et al.,* 2016). Además, la compactación del suelo puede reducir gran parte de la actividad microorganismos del suelo responsables en la mineralización fósforo orgánico en formas inorgánicas, una condición que afecta la difusión y flujo de este nutriente y reduce la habilidad de la absorción en las plantas (Kristoffersen *et al.,* 2015; Dorrough *et al.,* 2006; Tan *et al.,* 2008; Canbolat *et al.,* 2008; Subedi *et al.,* 2020). En este estudio el efecto positivo e interactivo entre las actividades ganaderas (AG) y el deterioro del hábitat (DH) sobre pH del suelo, sugieren que probablemente la liberación de cationes durante la mineralización del estiércol de ganado aumente el pH del suelo y promuevan la precipitación de P en formas no disponibles para las plantas (Dorrough *et al.,* 2006; Trejo-Escareño *et al.,* 2013).

En este estudio el método de "*Inferencia Lógica por Abducción"* y su aplicación en SEMs y criterios de información de Akaike facilito la búsqueda y selección de los indicadores ecológicos más plausibles para explicar el efecto de las actividades antropogénicas y de la modificación ambiental sobre la respuesta funcional foliar de las especies. Los cambios de diversidad funcional proporcionan una base para describir la variación en las estrategias del uso de los recursos en las plantas y los mecanismos de coexistencia (Tilman *et al.,* 1997; Grime, 1998; Garnier *et al.,* 2004; Loreau y Hector, 2001; Reich *et al.,* 2014; Hu *et al*., 2015; Mason *et al.,* 2016). Específicamente en este estudio, el incremento de las actividades de ganadería (AG) y sus efectos sobre la reducción del fósforo inorgánico del suelo mostraron un efecto negativo sobre la diversidad funcional de los atributos foliares en las malezas. En diferentes ecosistemas se ha demostrado que las actividades de ganadería y/o sus efectos sobre la reducción en la disponibilidad de nutrientes limitantes como el fósforo actúan como nuevos filtros de selección que promueven un efecto de convergencia funcional en el ensamblaje de especies; a través de los cuales se favorece gradualmente el establecimiento de especies de malezas con atributos funcionales similares (Stock y Verboom, 2012; Castro-Díez *et al.,* 2012; Kraft *et al.,* 2015; Funk *et al.,* 2016; Fried *et al.,* 2019; Wu *et al.,* 2020). Autores como Drenovsky et al. (2012b) y Funk et al. (2016) han propuesto en ecosistemas secos y templados que el efecto convergencia observado en los atributos foliares en las especies de malezas es el resultado de un efecto de selección que maximiza la captura de recursos y la tasa de asimilación de nutrientes en las hojas.

En este estudio, el método "*Inferencia Lógica por Abducción"* demostró que la media ponderada del área foliar (CWM. LA; community-weighted mean leaf area) es el indicador funcional más plausible para explicar la repuesta funcional de las malezas herbáceas a la reducción de fósforo inorgánico del suelo. Al igual que Leishman et al. (2007) y Hu et *al.* (2018) en este estudio se demostró que el área foliar (LA) es un atributo de crucial importancia para la habilidad competitiva de las especies de malezas que colonizan y se establecen en ambientes perturbados y con baja disponibilidad de nutrientes como el fósforo (inorgánico). Al respecto se ha informado que las especies de malezas presentan una mayor área foliar (LA; leaf area) en comparación con las especies características (Te Beest *et al.,* 2014; Funk *et al.,* 2017). Probablemente debido a que es un atributo relacionado con una estrategia de recursos adquisitiva, y favorece una mayor tasa fotosintética, captura de carbono

y asimilación de contenido de nutrientes en la hoja (Feng *et al.,* 2008; Moles *et al.,* 2008; Firn *et al.,* 2012; Funk *et al.,* 2016). Si bien, se podría esperar que los niveles deficientes de fósforo en el suelo afecten la formación de células que componen los tejidos vegetales; probablemente en el bosque de *A. religiosa* las especies de malezas presentan ciertas características que favorecen la asimilación de este nutriente (Ordoñez *et al.,* 2010; Gong *et al.,* 2020). Al respecto Vázquez- Santos et al. (2021) han demostrado en este bosque que la presencia de micorrizas arbusculares en la maleza *Acaena elongata* promueve una mayor asimilación de fósforo y asignación reproductiva en condiciones perturbación antropogénica y baja disponibilidad de fósforo.

Por el contrario de lo que ocurre en las especies de malezas herbáceas, el método "*Inferencia Lógica por Abducción"* demostró que la media ponderada del contenido de materia seca foliar (CWM.LDMC; community-weighted mean leaf dry matter content) es el indicador funcional más plausible para explicar la repuesta funcional de las malezas arbustivas al efecto interactivo de las actividades de ganadería (AG) y el deterioro del hábitat (DH). Si bien para la mayoría de las especies de malezas frecuentemente se observan atributos relacionados con una tendencia adquisitiva de recursos (LA; leaf area); autores como Funk et al. (2016) han reportado que las malezas arbustivas con un ciclo de vida más largo que las malezas herbáceas, favorecen la presencia de atributos relacionados con una tendencia de recursos conservativa. En las especies esta tendencia se ve representada por hojas que maximizan la acumulación de recursos, con alta resistencia estructural y que por lo tanto presentan un mayor contenido de materia seca foliar (LDMC; leaf dry matter content) (Brym *et al*., 2011; Guido *et al*., 2021). Estos atributos generalmente también se encuentran relacionados una alta cantidad de metabolitos secundarios en las hojas que forman compuestos alelopáticos y a través de los cuales se pueden producir cambios en el suelo que reducen las tasas de descomposición y el ciclo de nutrientes (Castro-Diez *et al.,* 2012). Al respecto en áreas altamente perturbadas del bosque de *A. religiosa,* se ha demostrado que la maleza arbustiva *Sambucus nigra* presenta un alto contenido de terpenos en sus hojas (Pineda-Romero, 2016).

En relación con las especies características de la vegetación, los modelos SEM demostraron que los incrementos del pH tienen un efecto positivo sobre la media ponderada

(CWM; community-weighted mean) del área foliar (LA; leaf area) y contenido de materia seca foliar (LDMC; leaf dry matter content) de las especies características. Así mismo, los resultados de los análisis RLQ demuestran que los incrementos de pH del suelo favorecen los aumentos de la cantidad de clorofila en las especies arbóreas características. Autores como Johnstone (2004) han mostrado que las actividades antropogénicas al promover la lixiviación de suelo frecuentemente generan cambios en las concentraciones de los cationes intercambiables que modifican las condiciones del pH del suelo. En este estudio el efecto positivo del pH del suelo sobre los atributos foliares en las especies características, probablemente se debe a que los valores de pH del suelo de los bosques de *A. religiosa* son más bajos (5,2 a 6,4 pH) de los valores que frecuentemente se requieren para promover una alta disponibilidad de nutrientes del suelo (pH 7,0; Härdtle *et al.,* 2004). De forma similar a nuestro estudio, Cregg *et al.,* (2004) y Gong y Gao (2019) han demostrado que las especies arbóreas dominantes de los bosques templados son altamente sensibles a las modificaciones del pH del suelo e inducen cambios fisiológicos sobre el sistema fotosintético y la tasa de asimilación de nutrientes en las hojas.

Si bien la aplicación de los SEM ya ha sido utilizada previamente en el desarrollo de indicadores ecológicos (Santibáñez-Andrade *et al.,* 2015; Fan *et al.,* 2016), en la mayoría se han asumido supuestos estadísticos que no siempre se cumplen en los ecosistemas (i,e., distribución normal). En este estudio la incorporación de los SEMs de nueva generación, los piecewiseSEMs (Lefcheck, 2016) en el método "*Inferencia Lógica por Abducción*" permitieron evaluar de forma eficiente relaciones de causalidad en un conjunto de datos con una distribución diferente a la normal. El paquete de R, piecewiseSEM introduce un marco matemático flexible que puede incorporar una amplia variedad de estructuras, distribuciones y supuestos en los modelos (Lefcheck, 2020). Estos incluyen: efectos fijos y aleatorios, modelos jerárquicos, y criterios de información de Akaike (AIC; Akaike information criterion) (Lefcheck, 2020). La incorporación de los valores AIC permiten la selección de los SEM más plausibles a partir de la comparación de un conjunto extenso de modelos probables, en contraste con la interpretación del valor *p* en los SEMs que buscan encontrar evidencia de las relaciones causales a partir de un solo modelo inicial (Shipley *et al.,* 2013; Lefcheck, 2020).

En esta tesis, la aplicación de los piecewiseSEM en el método "*Inferencia Lógica por*

Abducción" permitió realizar una predicción de la trayectoria de la comunidad a través de la evaluación del efecto antropogénico sobre indicadores ecológicos de la vegetación, el banco y la lluvia de semillas. En este punto es importante mencionar que la interpretación de los indicadores funcionales puede diferir en otros ecosistemas y por lo tanta la aplicación de este método en otros ecosistemas requiere un conocimiento profundo del sistema de estudio. Por ejemplo, en los ecosistemas secos, la estación seca puede ser un factor que promueve patrones de convergencia funcional, incluso en ausencia de perturbaciones antropogénicas (Lohbeck *et al.,* 2013).

Los resultados de este estudio demuestran que las actividades antropogénicas promueven un efecto de retroalimentación positiva que continuamente es alimentado por la entrada de semillas de especies de malezas con una alta variedad de atributos funcionales (Pakeman *et al.,* 2013). Específicamente las actividades de deterioro del hábitat favorecen la entrada de especies de malezas con una alta divergencia funcional (FDiv) en el banco y la lluvia de semillas. Probablemente, esto sucede porque las actividades de deterioro del hábitat, como la deforestación, eliminan los obstáculos para la dispersión de semillas de malezas y promueven la creación de nuevos microambientes (e.g., incrementos de luz y temperatura) que favorece su germinación. Mientras que en la vegetación los efectos combinados de las actividades de deterioro del hábitat con las actividades de ganadería funcionan como filtros de selección que favorecen el establecimiento de un número reducidos de especies de malezas con atributos y tolerancias similares (Marteinsdóttir, 2014; Tjelele *et al.,* 2015; de Moraes-Stefanello *et al.,* 2019).

Considerando que la capacidad de recuperación de los procesos del bosque de *A. religiosa* depende directamente de las especies presentes en el banco y la lluvia de semillas, nuestros resultados demuestran que la entrada de las especies de malezas promoverá cambios drásticos en el mantenimiento de los procesos y funciones. Los análisis RLQ del banco y la lluvia de semillas muestran que el incremento de los disturbios antropogénicos ocasiona el reemplazamiento de especies características arbustivas con síndromes de polinización por entomofilia, (e.g., flores tubulares), por especies de malezas tanto nativas como introducidas, con atributos relacionados con una estrategia de vida ruderal con una forma de crecimiento herbácea y que presentan una alta dispersión de semillas pequeñas. Bajo este escenario,

probablemente en el bosque de *A. religiosa* se promoverá un decremento de los procesos que integran la regeneración natural, como la polinización, la dispersión y el establecimiento de especies (Aizen y Feinsinger 1994; Cramer *et al.* 2007; Bonilla-Valencia *et al.,* 2017; Hooper y Ashtoon, 2020).

De acuerdo con los resultados de esta tesis se predice que la comunidad del bosque de *A. religiosa* tiene una baja probabilidad de recuperar su ensamblaje histórico o natural y por lo tanto, probablemente se conducirá hacia un estado alternativo estable, con un ensamblaje dominado por especies de malezas (Larson y Funk, 2016). Si bien actualmente existe un número creciente de estudios que han utilizado la teoría del estado estable alternativo para el manejo y la restauración en ecosistemas (Suding *et al.,* 2004; Walker y Salt 2012; Standish *et al.,* 2009), muchas de estas investigaciones se han centrado en la vegetación establecida (Suding y Hobbs 2009; Ma *et al.,* 2021), ignorando en gran medida el papel de los bancos y la lluvia de semillas en la resiliencia de los ecosistemas (Johnstone *et al.,* 2004; Bhattachan *et al.,* 2014). Al respecto autores como Gioria *et al.* (2021) han demostrado que las especies introducidas formadoras de banco tienen una alta capacidad para desempeñarse como especies invasoras, debido a que pueden permanecer largos periodos de tiempo almacenadas en el suelo y promover su germinación cuando se presentan condiciones ambientales favorables; tales como *Sigesbeckia jorullensis, Geranium seemannii, Cardamine hirsuta.*

En este estudio el sistema de retroalimentación positiva en el banco y la lluvia de semillas reduce la probabilidad de que se produzcan transiciones naturales de regreso al estado estable original (Ghazaoul *et al.,* 2015; Ma *et al.,* 2019; Ma *et al.,* 2021). Autores como, Ma *et al.* (2021) proponen que en estos ecosistemas las estrategias de conservación deben ser focalizadas en preservar a las especies características presentes en la lluvia y el banco de semillas. Para Ma et al. (2021) estas especies representan una fuerza impulsora latente que puede dirigir a las comunidades hacia un estado alternativo más deseable. En el bosque de *A. religiosa* la alta abundancia de especies características en la lluvia de semillas como *A. religiosa* (4,865) *y Brickellia scoparia* (3,410) proporcionan una ventana de oportunidad para mantener la resiliencia del ecosistema. Particularmente la regeneración de *A. religiosa*, así como de otras especies arbóreas que presentan bancos de semillas transitorios, depende directamente de la formación de bancos de plántulas en el suelo (Lara-González *et al.,* 2009).

En el área de estudio Aldana-Barrios *et al.* (2019) reporta para *A. religiosa* una alta presencia de plántulas (328) y brinzales (140). Condición que sugiere una buena capacidad de regeneración natural de *A. religiosa.* Por lo cual, se recomienda desarrollar planes de manejo y restauración focalizadas en la germinación, establecimiento y el monitoreo de esta y otras especies características de la comunidad. Esto con el propósito de prevenir transiciones hacia nuevos estados no deseables y evitar sus posibles costos ecológicos, económicos y sociales.

Así mismo, es importante considerar que durante la construcción de indicadores ecológicos basados en la diversidad funcional otros atributos pueden ser más relevantes. En este estudio, los indicadores se basaron en atributos funcionales "suaves" los cuales son de fácil medición (Thompson *et al.,* 2000; Lavorel y Garnier, 2002; Lozanzkova *et al.,* 2018; Glatthorn *et al.,* 2021). Sin embargo, es importante tomar en cuenta, que los indicadores también pueden ser construidos a partir de atributos "duros" los cuales son metodológicamente menos accesibles que los atributos suaves, pero relacionados más directamente con la respuesta funcional de las especies. Por ejemplo, la masa de semillas (atributos suaves) que se relaciona con la tasa de germinación (atributo duro) (Lozanzkova *et al.,* 2018; Zakharova *et al.,* 2019). Así mismo, también es importante considerar que durante la construcción de indicadores funcionales puede ser relevante determinar las relaciones filogenéticas de las especies. Esto debido a que muchas de las repuestas funcionales entre especies pueden ser más dependientes de las relaciones cercanas filogenéticas que de la respuesta inmediata a los factores de perturbación (Cavender-Bares *et al.,* 2004). Por lo tanto, el desarrollo de los indicadores basados en la diversidad funcional requeriría en el futuro del apoyo interdisciplinario de otras ramas.

Conclusiones generales

El método de *"Inferencia Lógica por Abducción"* y su aplicación a través de modelos SEM representan un avance en el desarrollo de los indicadores funcionales. A partir de este método fue posible integrar la complejidad del efecto antropogénicos y realizar la búsqueda de la métrica de diversidad funcional que mejor explica la respuesta de las especies a los factores de perturbación. Consecutivamente la aplicación de este método en la vegetación, el banco y la lluvia de semillas del bosque de *A. religiosa* demostró facilitar el desarrollo de indicadores de vulnerabilidad de ensamblaje (riqueza, diversidad funcional y composición). Por lo cual fue posible generar con ellos un sistema de alerta temprana de los cambios en la composición y función a futuro. Los resultados de este estudio demostraron que la comunidad presenta un sistema de retro alimentación positiva que constantemente favorece la entrada de malezas con una alta diversidad funcional en el banco y la lluvia de semillas. Bajo este escenario, la regeneración de las especies características probablemente se inhiba, y la trayectoria de la vegetación puede dirigirse hacia un nuevo estado alternativo estable. Situación en la cual probablemente se necesitarán actividades de restauración ecológica para recuperar la integridad funcional. Por lo tanto, este estudio abre la posibilidad de avanzar en el desarrollo de indicadores funcionales para integrar otros componentes de las comunidades como la complejidad estructural, así como incorporar otras herramientas estadísticas como el criterio de información bayesiano, que ha demostrado evaluar con éxito la diversidad funcional en estructuras jerárquicas. La aplicación de estos indicadores en otros ecosistemas degradados representa una oportunidad parar mejorar nuestra comprensión de la capacidad de resiliencia de los ecosistemas y promover la aplicación de nuevas estrategias de gestión, restauración y conservación.

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