Reviving revenant remnants:

guiding revegetation using metapopulation modelling for improving connectivity in a fragmented landscape

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Certificate of Originality

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing this thesis and all sources used have been acknowledged in this thesis.

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Preface

The thesis has been written in the style of thesis by publication. Four articles form the main body of the thesis: one published article and three prepared according to the style of *Landscape Ecology*. The articles have been prepared according to the publishing guidelines and word limits of the respective journals; hence, formatting is not consistent throughout the main body of the thesis. As Chapters 2 to 5 have been prepared as manuscripts, I apologise in advance for some repetition between chapters. However, it is an inevitable consequence of preparing the thesis in the format of a series of journal articles.

Chapter 2 has been published in *Biological Conservation* 195, 177–186 (Appendix 1)

Chapter 3 has been published in *Landscape Ecology* 32:1837–1847 (Appendix 2)

Chapter 4 has been prepared according to the style of *Landscape Ecology*

Chapter 5 has been prepared according to the style of *Landscape Ecology*

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Chapter 2
Planning for metapopulation persistence using a multiple component, cross-scale model of connectivity

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Chapter 3
Integrating a generic focal species, metapopulation capacity, and connectivity to identify opportunities to link fragmented habitat

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At the time of processing, no evidence of publication has been located for the following chapters, and accordingly these listed chapters have been retained in this version of the Thesis document:

Chapter 4
Validating a forward-looking metapopulation occupancy model using detection data reveals greater than expected disparity in habitat suitability

and

Chapter 5
How effective are local revegetation programmes in conserving biodiversity in fragmented landscapes?

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Abbreviations

BNB	Brigalow–Nandewar Biolinks
BRG	Border Rivers – Gwydir
CBA	cost–benefit approach
CMA	Catchment Management Authority
DECC	(former) Department of Environment and Climate Change
GFS	generic focal species
LLS	Local Land Services
LMDB	Land Management Data Base
MPC	metapopulation capacity
NRM	natural resource management
NSW	New South Wales
NTLLS	Northern Tablelands Local Land Services
NVMBA	Native Vegetation Management Benefits Analysis
NWLLS	North West Local Land Services
OEH	Office of Environment and Heritage
REMP	Rapid Evaluation of Metapopulation Persistence
SLT	Spatial Links Tool

Abstract

Habitat connectivity is vital for species population persistence but habitat loss and fragmentation is driving species decline across the globe. In order to respond to this challenge, conservation planners need ecologically relevant information to enable restoration of habitat and connectivity. The aim of this research was to use metapopulation theory and landscape ecology to provide biologically relevant guidance on how to improve landscape connectivity in a fragmented agricultural landscape, through an on-ground revegetation programme. In realising this aim, recently developed but not yet widely utilised methodologies were applied to a real-world conservation investment programme. These methodologies integrated concepts from metapopulation theory and landscape ecology to assess landscapes for their capacity to sustain viable metapopulations of a species of interest. A theoretical advance arising from this research was to develop the dispersal linkages as a stand-alone modelling component, hitherto a feature retained within the metapopulation model. New frameworks and syntheses of methodologies were developed in response to specific investment agency requirements but will have general application elsewhere.

The study was conducted in the Border Rivers – Gwydir catchment in northern New South Wales, eastern Australia, as part of the Brigalow–Nandewar Biolinks revegetation project. The regional economy of the study region is based around agriculture (grazing and dryland and irrigated cropping), and native vegetation has been extensively cleared and modified for this purpose, resulting in relictual, fragmented and variegated landscapes.

Chapter 2 describes how collaboration between spatial researchers and on-ground practitioners bridged the knowledge gap to deliver better-informed management options for investment in connectivity and biodiversity outcomes. The chapter describes a fit-for-purpose, cross-scale methodology consisting of multiple component models, where each component reflected varying

spatial scales. The objectives were to (1) develop a spatially explicit methodology for identifying and improving connectivity, and (2) provide natural resource management agencies with the knowledge base for implementing revegetation actions for maximum biodiversity benefit. The methodology was based on concepts of metapopulation ecology and landscape ecology and used least-cost paths analyses. At the wider scale, native vegetation extent and condition were used as surrogates for biodiversity; and at the finer scale, landscape structure and a focal woodland species group were used to derive generic movement parameters for determining least-cost paths. A hierarchical approach was used to derive priority revegetation zones where local priority zones for linking habitat were combined with regional-scale and sub-continental-scale conservation benefits zones. Revegetation in these areas is expected to efficiently increase access to resources for biota, increase dispersal potential and thereby enhance biodiversity persistence. The approach interpreted local management-mediated actions within a metapopulation persistence context. This approach has application in other geographical settings where opportunities exist to connect the implementation needs of NRM practitioners with scientific knowledge.

Chapter 3 expands the previous work by presenting a strategy to account for the widest possible spectrum of biodiversity in revegetation programmes in fragmented landscapes by incorporating multiple species occurrence and dispersal processes operating across spatial scales. The objective was to apply metapopulation theory to a fragmentation-sensitive woodland and forest specialist generic focal species (GFS) and predict landscape capacity, the distribution of persistent GFS populations and their potential dispersal pathways to highlight connectivity gaps between populations. Maintenance of populations could thereby be facilitated through re-connecting habitat networks across regional and broader scales, with assumed benefit for the dispersal needs of less fragmentation-sensitive species. Predicted occupancy and metapopulation capacity was derived from ten fragmentation-sensitive woodland birds, mammals and reptiles combined into the one GFS. A novel metapopulation connectivity analysis predicted regional

dispersal links to identify likely routes through which individuals could move to contribute to the viability of the population. Landscape capacity of the current landscape varied across the region. Low-value links between populations provided greatest opportunities for revegetation and improved landscape capacity. Where regional connectivity did not indicate a pathway between populations, broader scale connectivity provided guidance for revegetation. The metapopulation-based model, coupled with a habitat dispersal network analysis, provided a platform to inform revegetation locations and better support biodiversity. The approach has application for directing on-ground action to support viable populations, assess the impact of revegetation schemes or monitor the progress of staged implementation.

The objective of Chapter 4 was to gain insight into the relationship between two representations of habitat suitability—one indicated by past observations of species and the other being GFS-predicted occupancy—in order to influence restoration actions. Qualitative and quantitative methods were used to examine the GFS model. Observational records of the ten individual GFS species were visually assessed for overlap with the predictive model, and logistic regression was used to test the predictive GFS occupancy model against observations of the GFS species. This was followed by a series of sensitivity analyses in order to improve congruence between the predictions of persistent GFS occupancy and the observation. The observational data were biased and visual assessment revealed many observations of one species, grey-crowned babbler (*Pomatostomus temporalis*), where no occupancy was predicted. Logistic regression showed the current GFS observations and predicted occupancy were not well aligned and their congruence could not be improved by altering parameter values in the sensitivity analyses. The reason for this is unclear; however, these results are predicated on incomplete, biased observational records and likely lag effects due to a probable extinction debt, making the metapopulation model difficult to test. The lack of agreement indicates that, based on landscape considerations only, the landscape required for persistence of woodland species differs from that

which is currently supporting occupancy. Actions to improve habitat connectivity are therefore required. The metapopulation model could be improved by incorporating a new habitat suitability surface derived from observation data into the calculation of persistence.

Reporting on the performance and expected benefits of restoration actions is uncommon and the elements of success can be difficult to define and measure. Consequently, Chapter 5 was an evaluation of revegetation works undertaken from 2012–2016 by the natural resource management agencies in the study region. The evaluation was a novel application of a metapopulation approach rather than the more common survey of site-based attributes. The assessment was framed around two research questions: (1) did the design of the revegetation patches conform to aspects known to influence biodiversity response to revegetation, and (2) was revegetation located where it had the potential to contribute greatest benefit to biodiversity? The potential for the plantings to improve biodiversity was determined from the cross-scale connectivity and benefits mapping presented in Chapter 2 and the best-parameterised GFS metapopulation model from Chapter 4. Evaluation was predicated on the assumption that greatest biodiversity benefit would arise from plantings located in the intermediate range of the spatial assessment themes. Plantings were dominated by small patches with high area–edge ratios. However, none of the patches was beyond the distance considered maximal for dispersal of woodland birds and mammals, and most sites were within the distance of daily forays. The majority of revegetation area was located within high priority zones for revegetating, such as cleared areas or areas identified for improving existing remnants. However, this positive assessment was overshadowed by the highly fragmented natured of the landscape, resulting in substantial amounts of revegetation established where it was predicted to have minimal potential for improving regional biodiversity in the long term. Much additional restoration work—either more numerous revegetation patches or larger-sized patches, and cognisant of landscape context—is required to make potential gains in landscape connectivity and species occurrence.

In conclusion (Chapter 6), the study found that options for guiding revegetation varied according to the extent of habitat modification and the resulting landscapes: relatively intact, fragmented or relictual. Connectivity was considered sufficient for biodiversity persistence in relatively intact landscapes but revegetation is urgently required in relictual landscapes where an extinction debt is likely playing out. Opportunities for linking populations were more obvious in fragmented landscapes where isolated populations and weak dispersal links were identified. Although best available data was used in the analysis, there were limitations in the spatial data and in the parameter values of the GFS. Improvements could be made trialling alternative habit condition layers or testing the approach in alternative regions to better assess the predictive metapopulation model. The analytical approaches taken in this thesis can be adopted by NRM agencies for identifying locations for revegetation and for adaptively managing programmes through monitoring and evaluation. Evaluation of revegetation efforts undertaken by the NRM agencies to date reveal the works will be insufficient for improving species persistence at a regional scale. Revegetation activity is at too small a scale and situated in inadequate locations for significantly increasing species occurrence or population viability across the region. Although some species are expected to benefit from recent revegetation, without increased and sustained effort species will continue to be lost from the region. Continuing collaboration between researchers, NRM agencies and rural communities is recommended to help with this problem.

Chapter 1

Introduction

1 Background

Across the globe, increasing human demands for services such as food and fibre are driving ever-increasing rates of anthropomorphic change to natural landscapes (MEA 2005; Tilman et al. 2011). The expansion of cropping and grazing is a major contributor to the clearing and converting of natural ecosystems, which is profoundly affecting ecosystem services and the maintenance of biodiversity (Scherr and McNeely 2008; Lindenmayer et al. 2012; ASE 2016; Fischer et al. 2017). Biodiversity and ecosystem function supplies a range of services to productive agricultural landscapes, and also have their own intrinsic value as part of the natural world (Fischer et al. 2006; Batavia and Nelson 2017). However, when agriculture dominates a landscape it can result in fragmentation and isolation of natural habitats, breaking formerly contiguous ecosystems and populations of native species into smaller patches, making them vulnerable to extirpation. Alternatively, agricultural practices can produce variegated landscapes where habitat is variously modified rather than destroyed and species that are particularly sensitive to exogenous disturbance are restricted to the least modified habitat (McIntyre and Hobbs 1999). Fragmentation and landscape modification are a major threat to biodiversity (Hanski 1999; Soulé et al. 2004; Fischer and Lindenmayer 2007) and in agricultural landscapes there is an urgent need to reconcile conflicting perspectives of land use and food security (McIntyre 1994; Henle et al. 2008; Phalan et al. 2011; Kueffer and Kaiser-Bunbury 2014; Mouysset et al. 2015; Fischer et al. 2017).

An extensive literature has developed around the impact of landscape modification and fragmentation—and reduced connectivity—on biodiversity (Bennett 1990; Saunders et al. 1991; Hobbs and Norton 1996; McIntyre and Hobbs 1999; Bennett et al. 2006; Ansell et al. 2016b). Habitat removal reduces the total area of habitat available to species and isolates the remaining remnants from one another, with the degree of isolation determined by the connectivity and permeability of the intervening landscape or matrix (Saunders et al. 1991). Matrix permeability is the extent to which the elements of the landscape either allow or encourage animal movement (Kuefler et al. 2010). If habitat patches are connected insufficiently to enable this movement, species persistence across the landscape can be compromised; it is therefore important to manage the matrix to improve or retain connectivity (Schmiegelow 2007; Ruffell et al. 2017).

In heavily fragmented landscapes, restoration of connectivity is required if reinstating communities and functioning ecosystems, including maintaining and restoring biodiversity, is to be achieved (Soulé et al. 2004; Henle et al. 2010). Connectivity is also needed as an adaptation measure for climate change, allowing species and whole communities to migrate to emerging habitats as others disappear (Driscoll et al. 2014; Watson et al. 2017).

However, the concept and practice and of restoring connectivity has been controversial (Hodgson et al. 2009), in particular with regard to the potential negative consequences of linkages such as corridors (Bennett 2003). Identified concerns include: spreading pathogens, parasites and exotic species such as pests, weeds and predators; facilitating the spread of disturbances such as fire; introducing new genes, which could disrupt local adaptions and co-adapted gene complexes (‘outbreeding depression’); promoting hybridisation between previously disjunct populations; increasing exposure of animals to predators or other sources of mortality (‘mortality sink’); creating habitat sinks in which mortality exceeds reproduction, thereby draining regional populations; and creating a trade-off between alternative conservation measures such as land acquisition or enlarging core areas (Bennett 2003; Crooks and Sanjayan 2006). On balance, it is

thought that the benefits of connectivity outweigh these potential problems in most situations (Bennett 2003). Moreover, environmental problems are most likely to accrue in linkages that attempt to link areas not naturally connected, and a specific negative consequences may not affect all organisms (Bennett 2003; Collinge 2009).

A challenge for conservation planning in agricultural landscapes is to deliver effective conservation outcomes and agricultural production concurrently (Bennett at al. 2006). This requires targeting limited conservation investment funds to where they will have greatest benefit (Hajkowicz 2009; Bryan 2010).

This study was conducted in the Border Rivers – Gwydir catchment in northern New South Wales (NSW), eastern Australia, as part of the Brigalow–Nandewar Biolinks revegetation project (NTLLS 2017). The aim of the project was to establish 1,550 ha of revegetation for the improvement of landscape-scale connectivity and to increase the extent of riparian vegetation. The native vegetation in the region has been extensively cleared and modified for agriculture and grazing. Habitat fragmentation is now considered a key threat to the remaining biodiversity in the region. Since European settlement, 71% of the community structure, composition and regenerative capacity of the region's native vegetation has been significantly altered by land use or land management practices (DECC 2010). The region has 149 species listed as threatened under the NSW *Threatened Species Conservation Act 1995*, consisting of 67 plant species, and 46 bird, 24 mammal, five reptile, six frog and one invertebrate species. Sixteen threatened ecological communities occur in the region, including brigalow (*Acacia harpophylla*), weeping myall (*A. pendula*) woodland, semi-evergreen vine thicket, box–gum (*Eucalyptus spp.*) grassy woodland, natural grassland on alluvial plains, New England peppermint (*E. nova-anglica*) woodland, coolibah (*E. coolabah)* – black box (*E. largiflorens*) woodland and upland wetlands (NSW OEH 2013). A total of six of these species and ecological communities are listed as critically

endangered under the federal *Environment Protection and Biodiversity Act 1999* (NSW OEH 2013).

The following literature review discusses the concepts relevant to the research, namely landscape change and connectivity. The review also addresses the role of modelling, and planning for ameliorating habitat loss through improving connectivity and revegetation in agricultural regions. The last section of this chapter presents the general aim of the research, the thesis objectives and the sequence of the chapters. The reader is referred to the glossary for definitions of terms and concepts used throughout this thesis.

2 Literature review

2.1 Introduction

As stated above, intense human use of natural landscapes, whether for food production, urbanisation, industry or resource extraction, has resulted in the fragmentation of habitat. The outcome of habitat fragmentation, and the associated loss of habitat and the degradation of the remnants, has led to a dramatic decline in native species worldwide and is a major threat to biodiversity and its persistence (Saunders et al. 1991; Wilcove et al. 1998; MEA 2005; ASE 2016; Newbold et al. 2015).

Fragmentation and habitat loss affect the ability of species to respond to stressors such as environmental stochasticity and natural disasters such as flood, fire and drought, all of which are expected to be exacerbated by climate change (Fischer and Lindenmayer 2007; Araújo 2009; Crossman et al. 2012). Fragmentation and habitat loss also degrade habitat condition (Ford et al. 2009). The magnitidue and type of impacts are species-specific and vary widely across taxa due to different behavioural responses, making it difficult to identify a single consistent response to fragmentation (Debinski and Holt 2000). For instance, some of the effects include reduced reproductive success in orchids (Newman et al. 2013), declines in woodland birds (Bennett and

Watson 2011), reduced dispersal rates for small-leaved lime (*Tilia cordata*) (Collingham and Huntly (2000), and declining populations of native bush rat (*Rattus fuscipes*) in small habitat remnants (Holland and Bennett 2010). The survival of species and populations depends on their ability to access resources in each stage of their life cycle (Dunning et al. 1992) and to be able to respond to changing environmental conditions; this is conditional on individuals being able to disperse to new habitat. Successful dispersal is achieved when the individuals move easily about the landscape in order to reach new habitat, and is vital for species survival (Kindlmann and Burel 2008). There is often a considerable time lag between habitat loss and fragmentation and local extinctions—over generations—and this lag has been referred to as the extinction debt. Extinction debt has been defined as time-delayed but deterministic extinction; a future ecological cost from current habitat alteration (Tilman et al. 1994).

2.2 Landscapes in metapopulation ecology and landscape ecology

A landscape refers to the landforms of a region and its associated habitats at scales of hectares to many square kilometres, or more simply, a spatially heterogeneous area (Turner 1989). Landscapes are characterised by four main features: (1) landscape structure, or pattern (derived from the landscape elements); (2) landscape composition (the kind of elements that make up the landscape); (3) landscape function or processes (how spatial structure effects the movement of organisms and other materials), and (4) landscape change (the dynamic nature of both structure and function) (Turner 1989; Dunning et al. 1992; Hobbs 1994; Wiens 2002; Fu et al. 2011).

The descriptions of landscapes subject to fragmentation have varied. Landscapes have been classified as patches of habitat separated by a matrix of inhospitable non-habitat (Hanski 2008). This classification of landscapes dominates metapopulation theory (Hanski 1998; Hanski and Ovaskainen 2003) and island biogeography (Wilson and MacArthur 1967), where the matrix is viewed as hostile non-habitat and an impermeable barrier to species movement (Schmiegelow 2007). However, this framework is not always appropriate (Fischer and Lindenmayer 2007). An

alternative view espoused in the field of landscape ecology considers the matrix to provide a continuum of habitat and resistance to movement to better patches (McIntyre and Barrett 1992; Forman 1995; McIntyre and Hobbs 1999; Ricketts 2001). The degree of habitat destruction and modification determines if the landscape is intact, variegated, fragmented or relictual (McIntyre and Hobbs 1999) and what might appear as a structurally fragmented landscape may operate as a functionally variegated landscape. The matrix surrounding the remnant vegetation can have a strong influence on species occurrence and be more important than the size and arrangement of remnant patches (Driscoll et al. 2013). The level of utility of the landscape depends on the variety of species in the landscape, as each taxon uses the landscape's resources at different spatial scales (Lord and Norton 1990; McIntyre and Hobbs 1999). These concepts represent a continuum along the spectrum of pattern-oriented landscape change (McIntyre and Hobbs 1999; Fischer and Lindenmayer; Brudvig et al. 2017).

2.3 Connectivity in metapopulation ecology and landscape ecology

Metapopulation theory and landscape ecology each feature the concept of connectivity and species movement (Moilanen and Hanski 2001; Wiens 2006; Kool et al. 2013). Landscape ecological studies focus on the effects spatial patterning and changes in landscape structure (e.g. habitat fragmentation) have on the distribution, movement and persistence of species (Turner 1989).

Metapopulation theory emphasises the effects of space, species movement, and local extinctions and colonisations of local populations on the persistence of the metapopulation (Moilanen and Hanski 1998; Eaton et al. 2014). In the patch–matrix landscape perspective of metapopulation theory, connectivity deals with the emigration and immigration of species from one patch to the next (Moilanen and Hanski 2006; Moilanen 2011; Wiens 2006). The theory has two key premises: 1) populations are spatially structured into assemblages of local breeding populations, and 2) migration among local populations has some effect on local dynamics,

including the possibility of population re-establishment following extinction (i.e. some patches remain unoccupied at any one time; Hanski 1997, 2004). The theory makes the assumption that suitable habitat for the species occurs as a network of idealised habitat patches, varying in area, degree of isolation (or connectivity) and quality and existing among a swathe of unsuitable habitat (Hanski 1998).

By comparison, landscape ecology emphasises the entire landscape and how the characteristics and structure of the landscape as a whole affects the movement of populations, disturbances (natural and human) and materials, with the result that a connected landscape facilitates movement from one location to another (Wiens 2006). ‘Landscape connectivity’ was defined as the degree to which the landscape facilitates or impedes movement amongst resources patches (Taylor et al. 1993), but as understanding of systems changed to include the continuum concept of landscape change, and the role and permeability of the matrix, the definition has been refined and expanded (Kool et al. 2013). Connectivity is now defined as the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure (With et al. 1997) or simple as a ‘measure of easiness of movement’ (Kindlmann and Burel 2008). Therefore, landscape connectivity is the relationship between an organism and its environment; it conceptualises the dependence of species dispersal on landscape structure and matrix features, and is best viewed from a species-centric perspective (McIntyre and Hobbs 1999; Mairota et al. 2011).

Connectivity is classified as structural or functional. Structural connectivity is based on physical landscape elements such as patches, corridors and stepping stones, and does not consider behavioural responses of an organism to landscape structure (Calabrese and Fagan 2004; see Kindlmann and Burel 2008). It may also be described as the physical characteristics of the landscape between patches of occupied habitat (Doerr et al. 2011). Functional connectivity, on the other hand, considers the behavioural response of an organism (such as dispersal capacity) to

individual landscape elements and the element's spatial configuration (King and Width 2002). Structural connectivity can contribute significantly to functional connectivity (Doerr et al. 2011) but structural connectivity does not guarantee functional connectivity, although this assumption can be made mistakenly (Taylor et al. 2006; Saunders 2007). For instance, constructing a corridor, such as a linear link, between two apparently similar patches does not ensure species will move between the patches (Hobbs, 1992; Beier and Noss 1998).

There are two categories of functional connectivity: potential and actual (Calabrese and Fagan 2004). Potential connectivity combines physical attributes of the landscape with estimates of dispersal ability to predict the species-specific level of landscape connectedness. Potential connectivity allows for limited field data to be combined with modelling (Kindlmann and Burel 2008). Actual connectivity extends potential connectivity by combining physical attributes with observed dispersal between patches or through the landscape (Calabrese and Fagan 2004).

Descriptions of connectivity which fail to take into account variegated habitats fail to acknowledge the variable permeability of the matrix to species movement; the matrix is rarely uniformly to movement and isolation of habitat is more than the distance between patches (Donald and Evans 2006).

In addition to being species-dependent, connectivity is dependent on scale and process (Crooks and Sajayan 2006; Kool et al. 2013). Metapopulation processes of dispersal, foraging, immigration into new habitat and emigration from original habitat are influenced by the distances between habitat patches, habitat quality and the quality of the matrix (Saunders et al. 1991; Baguette and Van Dyck 2007; Watling et al. 2011). The influence of these variables vary according to a species' perception of heterogeneity, which will vary according to the perception of scale (Kotliar and Wiens 1990). The movement distances for these processes vary for an individual species and between different species; consequently, the same landscape can provide a range of different movement opportunities (Turner 2005). Because of this dependency, a single

landscape presents alternative levels of connectivity for different species, and the degree of connectivity can change through times (e.g. seasonally; With et al. 1997; Calabrese and Fagan 2004; Kindlmann and Burel 2008). Any assessment of fragmented landscapes, therefore, cannot be fully achieved without investigating its effects across multiple scales (Levin 1992; Noon and Dale 2002; Cushman et al. 2015; Rayfield et al. 2016).

Metapopulation ecology and landscape ecology share a focus on habitat structure and species movement (approached differently) but metapopulation ecology assumes all patches used by the species are equally suitable, embedded in an equally unsuitable, featureless matrix. Landscape ecology, conversely, embraces the complexity of mosaics found in real landscapes (e.g. variegated habitat configurations rather than a binary perspective) but without consideration of population dynamics (e.g. extinction and colonisation; Hanski 1997, 1998; Weins 1997). It was recognised early that there would be advantages in synthesising the two theories, particularly if the consequences for species of altering landscape characteristics were of interest (Weins 1997). The solution to the integration problem necessitated new perspectives on analytical techniques. For example, graph theory (Urban and Keitt 2001) provides a method to identify paths between occupied patches based on dispersal distances and has obvious relevance to spatial metapopulation models.

2.4 Population persistence and connectivity networks

A connected landscape does not guarantee persistence, nor does connectivity equate to persistence (Moilanen and Hanski 2001; Taylor et al. 2006; Moilanen 2011). Persistence is the result of various factors, including metapopulation processes, and while landscape connectivity contributes to movement patterns, it does not shed light on births or deaths (Moilanen 2011). To measure persistence, other measures such as metapopulation capacity (Hanski and Ovaskainen 2000), rapid evaluation of metapopulation persistence (Drielsma and Ferrier 2009) or spatial population viability analyses (Akcakaya 2000) are required. These measures integrate necessary

information including habitat requirements, population size, dispersal, movement patterns, and birth and death rates with spatial landscape pattern (Schmiegelow 2007; Moilanen 2011).

However, the objective of strategies designed to create networks of linked habitat is to facilitate persistence through the movement of individuals between populations, for which there has been some evidence of increased persistence (Bennett 2003; Baguette et al. 2013). Linkages to restore or maintain connectivity are frequently comprised of corridors and stepping stones (Beier and Noss 1998; Bennett 2003). Corridors, usually linear features, can be contiguous stretches of habitat connecting larger habitat patches or composed of stepping stones. Stepping stones are a series of smaller patches or scattered trees separated by less favourable habitat but which remain accessible during landscape-wide movements (Fischer and Lindenmayer 2002; Scotts and Drielsma 2003; Baker and Fuller 2013; Bennett 2003). Stepping stone corridors may be evident only at broader scales (Drielsma et al. 2007). Corridors may also occur between non-linear arrangements of habitat fragments where the gaps provide limited permeability (Drielsma et al. 2007). Corridors and stepping stones can be naturally occurring or re-instated through revegetation, which is the deliberate planting of, or regeneration of, predominantly native trees, shrubs and other plants in areas formerly cleared of their usual vegetation (Reid et al. 2009).

Historically, there has been an emphasis on conserving or managing large remnant patches. This is based on the concept of species–area relationships, where larger patches typically support more species than smaller ones and are less affected by disturbances or edge effects (Lindenmayer and Fischer 2006). However, this perspective ignores the potential importance of smaller patches in retaining species in the landscape, particularly in regions which have experienced extensive modifications (Lindenmayer and Fischer 2006), and in their contribution to stepping stone corridors. In Australia, where at least 22% of major vegetation communities have >50% of their remaining extent in patches <1000 ha, ignoring small patches in conservation planning can be a significant omission (Tulloch et al. 2017).

2.5 Planning landscape connectivity restoration with a focus on agricultural lands

Active restoration for improving connectivity and biodiversity as a remedy for excessive land clearance is undertaken in many parts of agricultural Australia (Soulé et al. 2004; Worboys and Pulsford 2011; Whitten et al. 2011; Fitzsimons et al. 2013; Norton and Reid 2013; and see Lindenmayer et al. 2010). However, plans to reduce or minimise the impacts of fragmentation need to be practical and meaningful if landscapes are to remain ecologically productive, with stakeholders engaged and investment accountable (Seddon et al. 2011; Lindenmayer et al. 2013; Adams et al. 2014; Auerbach et al. 2014; Mitchell et al. 2015; Ansell et al. 2016a; Riemann et al. 2017).

One challenge for restoration is where to locate activities (Hobbs and Kristjanson 2003; Holl and Aide 2011; Thomson et al. 2009; Wilson et al. 2011; McRae et al. 2012). There is consensus that decisions and methodologies should focus on landscape-scale perspectives, if not beyond (Soulé et al. 2004; Worboys et al. 2010). The extent of environmental decline also dictates that conservation and restoration actions need to span public and private tenures. Relying on reserves and governmental agencies alone will be insufficient for the challenge of conserving biodiversity (Noss 1983; Schmiegelow 2007; Margules and Pressey 2000; Worboys et al. 2010); public involvement is, therefore, essential (Recher and Lim 1990; Saunders 1990; Ansell et al. 2016b; Drielsma et al. 2016). Revegetation strategies, including managing for and re-creating connected systems, need to think beyond the farm boundary. The responses and requirements of different species will not be met within a single property and regional frameworks and stakeholder coordination will be required (Bennett 1995; Knight and Landres 2002).

When specific information is absent, general principles can be applied to revegetation actions aimed at reducing fragmentation and improving connectivity (Bennet and Mac Nally 2004); for example, ‘bigger is better’ or ‘connected is better than isolated’ (Hobbs and Norton 1996).

However, general principles do not allow for comparative studies between alterative habitat configurations and give no indication of species responses to specific interventions. Modelling can improve on an approach based on first principles by increasing understanding of complex systems over different temporal and spatial scales (Urban 2005; McGarigal et al. 2016). In addition, in the age of the Anthropocene, modelling allows for greater understanding of human intervention in ecological systems (Seidl 2017). Models are used when it is impossible or impractical to obtain geographically complete empirical data, when existing data is limited, or when predicted outcomes are required, for example to locate critical regions where functionality (e.g. connectivity) would be lost under changed land use (Lookingbill et al. 2010). The advantages of models include their ability to reduce the amount of cumbersome and intensive field surveys, predict a future state under different management programmes, assist decision making due to the capacity of models to deal with uncertainty and complexity, and forge greater links between science and management (Walters and Holling 1990; Beissinger et al. 2006; Addison et al. 2013). Additionally, ecological responses to landscape change occur at broad scales and over long time periods. This contrasts with the short time frames in which managers often need to make decisions (e.g. the annual budgetary cycle of agencies, and the 3–4 year electoral cycle of governments and their funding programmes; Addison et al. 2013).

Various models and frameworks are used for connectivity or restoration planning (Lethbridge et al. 2010). They vary in approach, metrics and the spatial scale of concern. Key conceptual variables used include habitat suitability, habitat reachability, restoration cost and biological behaviour (e.g. dispersal). Techniques range from stakeholder preferences (Zerger et al. 2011), to landscape metrics describing the spatial arrangement of habitat patches (Westphal et al. 2007), to more complex spatial tools and mathematical programming techniques for connectivity or restoration planning. These tools and mathematical approaches are usually derived from two bodies of literature: reserve design and corridor design (Alagador et al. 2012). The most

widespread reserve selection strategy is target-based, referred to as systematic conservation planning (Margules and Pressey 2000) or spatial conservation prioritisation (Pouzols et al. 2012), where targets are specified for biodiversity features and sites are selected to either meet the targets with least cost, or to maximise the number of targets met with given resources (e.g. money or area; Moilanen 2007). The most common approaches to solving these problems are integer-linear programming and simulated annealing (Beyer et al. 2015). The reserve approach, as the name suggests, was originally developed for designing protected area networks but is increasingly being used for prioritising areas for restoration and improving connectivity. Examples where simulated annealing has been applied to restoration include ecosystem restoration (Adame et al. 2015) using Marxan (Ball et al. 2009), restoring habitat amount and configuration for population persistence (Crouzeilles et al. 2015 using Marxan in conjunction with a metapopulation metric for connectivity, and OPRAH (Lethbridge et al. 2010), a tool designed specifically for optimising habit restoration. Integer-linear programming has been applied to forest restoration priorities (Orsi et al. 2011). An additional planning tool is Zonation (Moilanen et al. 2005), which couples reserve design and metapopulation concepts to rank locations for conservation action using a 'cell-removal' rule. It has been used to rank locations for revegetation (Thomson et al. 2009).

The design of corridors for landscape connectivity emphasises the connection between two or more existing protected areas (or habitats) and maps the linkages (Alagador et al. 2012; Cushman et al. 2013b). Least-cost paths, part of graph theory (Urban and Keitt 2001), is the most commonly used technique to map the linkages but other graph theory techniques include circuit theory and resistant kernels (Alagador et al. 2012; Cushman et al. 2013b). Other techniques relevant to connectivity planning include percolation theory (and the associated neutral landscape models; With 2002) and stochastic dynamic programming (Westphal et al. 2003). Examples where corridor design has been used for maintenance and restoration planning include: assessing connectivity at fine spatial scales over large spatial extents (Lechner et al. 2015, using least-cost

paths from the software Graghab and circuit theory in Circuitscape); assessing the practitioners' perspective of the utility of corridor design derived from graph theory (Bergsten and Zetterberg 2013); developing genetic corridors for the maintenance and restoration of habitat patches for species management (Creech et al. 2014, using least-cost paths in PATHMATRIX); and evaluating the effect of alternative revegetation options on metapopulations (Westphal et al. 2003, who used stochastic dynamic programming, and Taylor et al. 2016, who used least-cost paths and resistant kernels in the software REMP).

Recent developments have seen the merging of both reserve and corridor design approaches for greater application in spatial conservation planning, including habitat restoration. Examples include extending Zonation to include establishment of species-specific corridors in spatial conservation prioritisation (Pouzols and Moilanen 2014) and planning for climate change (Albert et al. 2017).

The focus for restoration planning may be single species or groups of species, treated as either surrogates or focal species (Boone and Krohn 2000; Pearce and Ferrier 2001; Ferrier 2002; Marcot 2006; Bryan 2010; Rabinowitz et al. 2010; Watts et al. 2010; Alagador et al. 2012, Cushman et al. 2013a; Tambosi et al. 2014; Crouzeilles et al. 2015; Polyakov et al. 2015; Poniatowski et al. 2016). Surrogacy is the use of a process or element (for example a species, ecosystem, or abiotic factor) to represent another aspect of an ecological system, often a management goal such as maintaining biodiversity (Hunter et al. 2016). The focal species approach (Lambeck 1997) identifies known threatening processes (e.g. fragmentation) in a given landscape, followed by identifying the species most sensitive to each threat. One or more species may be identified for each threat. It is argued that tailoring management options to minimise the threat to these focal species will cater for those species which are less affected by the threat. The focal species approach has been used successfully in connectivity assessments (Noss 2007), to guide habitat restoration and revegetation (Brooker 2002; Freudenberger and Brooker 2004) and

in planning for persistence of multiple species in reserve systems (Nicholson et al. 2013). Modelling specifically for candidate locations for revegetation to improve connectivity has employed the use of either surrogates, to represent either biodiversity or a species of interest (Thomson et al. 2009) or focal species (Huggett 2007; Brooker 2002; Doerr et al. 2013; Watson et al. 2001).

The focal species approach is not without its critics. Issues include the difficulty in identifying all threatened and declining species in an area and their limiting factors before then deciding on the focal species. Importantly, and in respect to fragmented habitat, there is no consideration of the effect of the matrix (Beier et al. 2008). There may also be a reluctance in basing conservation action on a single species (Lindenmayer et al. 2002; Lindemayer and Fischer 2003; Beier et al. 2008). The concept of a 'generic focal species' (Watts et al. 2010) was therefore developed to address some of the issues. This approach combines multiple characteristics of a group of species, sensitive to a particular threat, into a virtual species; the generic focal species is not a living species. The approach was not designed to represent a single existing species as it would be unrealistic to expect one species to exhibit the range full range of characteristics of the group. The generic focal species approach utilises sensitive, real species to enable an evaluation of how well a landscape would support a broader range of species, and to alleviate the need for many individual species analyses.

The final choice of approach depends, in part, on the goal of the planning activity and the capacity of stakeholders to implement the approach (Bergsten and Zetterberg 2013; Bower et al. 2017). Ultimately, however, the decision should be guided by the primary purpose of conserving or restoring viable populations that are resilient to current and potential future conditions (Noss et al. 2009). It is in this context that a metapopulation approach may be most appropriate, particularly for general biodiversity in fragmented landscapes, where isolated populations cannot be expected to survive without the successful operation of metapopulation dynamics and where

population connectivity is critical (Hanski 1998; Cushman et al 2013). Hence, if management decisions aim to enhance the persistence of species and populations in fragmented habitat, metapopulation models provide the architecture for integrating biological movements and spatial configuration of habitat (Akcakaya 2000; Akcakaya et al. 2007; Drielsma and Ferrier 2009; Nicholson and Ovaskainen 2009). Metapopulation models have been constructed for single species, multiple species or surrogates, and tailored towards reserve selection (e.g. Nicholson et al. 2006), species-specific corridor design (e.g. Creech et al. 2014) and design of compensation payments for conservation (e.g. Drechsler 2007). There are few frameworks which use metapopulations to investigate habitat restoration scenarios (but see Westphal et al. 2003; Thomson et al. 2009) and they are rarely applied in real-world conservation (Nicholson and Ovaskainen 2009). Alternative frameworks which do not incorporate metapopulations explicitly have also been proposed for restoration planning, for example, multi-criteria decision analysis (Bryan and Crossman 2008) and mathematical prioritisation using a combination of variables such as conservation goals, cost, likelihood of restoration and landscape features (Crossman et al. 2007; Wilson et al. 2011). However, as previously stated, maintaining population persistence and explicitly including such considerations is preferred as the final choice of approach for connectivity planning.

Recent developments in planning for restoration may combine metapopulation considerations, species-specific habitat availability and systematic conservation prioritisation techniques as separate elements in a framework designed to meet targets at minimal cost. For example Crouzeilles et al. (2015) mapped priority habit patches that would improve population dynamics, and Albert et al. (2017) used short range connectivity as a surrogate for the carrying capacity of a metapopulation. Alternatively, all elements may be integrated into a single software tool for mapping and prioritising corridors (Pouzols and Moilanen 2014). In all examples, population distribution is implied in the high value habitat patches but these approaches do not offer a

spatially explicit answer to locating populations, or the likelihood of their persistence. However, to ensure viable populations, such information, and associated connectivity between populations, is desirable.

Rapid evaluation of metapopulation persistence (REMP) (Drielsma and Ferrier 2009) is spatially explicit population software that integrates landscape connectivity with existing analytical techniques for determining the metapopulation capacity (persistence) of a given landscape and for predicting occupancy patterns within the landscape. In this regard, REMP differs from prioritisation approaches where species occurrence is implied. REMP also does not require the setting of targets or goals. Although persistence is a principal of systematic conservation planning and prioritisation, targets are generally not evaluated in terms of probability of persistence (Beyer et al. 2015). Another advantage of REMP is that it recognises the variegated nature of landscapes, particularly agricultural landscapes, by utilising grid cell data rather than viewing the landscape as a series of patches (habitat and non-habitat patches). Finally, REMP is a decision-support tool, rather than directing action from top-down, as prioritisation or optimisation approaches might. In the real world, social, economic and political constraints often influence choices in conservation planning. Combining ecological knowledge with landholder preferences and other policy objectives, under the rubric of 'informed opportunism' (Ikin et al. 2016), may create greater opportunities for uptake of the results of the analysis.

The acknowledged gap between scientists and practitioners of conservation actions, often referred to as the 'knowing–doing' gap, is a limitation to effective on-ground conservation interventions in agricultural landscapes (Prober and Smith 2009; Hulme 2014). Studies that lead to on-ground implementation are not well reported, despite the availability of technical knowledge (but see Bryan 2010). Reporting on the performance and expected benefits of programmes is also uncommon (Jones et al. 2013; Duncan and Reich 2016), despite the development of frameworks designed for monitoring landscape-scale conservation management initiatives (Bellamy et al.

2001; Lindenmayer and Likens 2009; Nilsson et al. 2016; Watson et al. 2017) and the importance of monitoring and evaluation generally (Margoluis et al. 2013).

3 Thesis objectives

The challenge for those investing in conservation actions is knowing where to achieve the best returns for biodiversity from limited resources. The need for metapopulation and landscape ecology theories to be combined to adequately account for the influence of landscape characteristics on population persistence has been established above. These dual positions present an opportunity for collaboration between scientists and practitioners, where ecological concepts might inform or direct those investment choices.

Thus, the aim of this research was to apply metapopulation theory and landscape ecology to provide biologically relevant guidance on how to improve landscape connectivity in a fragmented agricultural landscape. This was applied to a real-world on-ground revegetation programme. This novel research synthesises a suite of connectivity analyses to cater for the connectivity requirements of multiple species across multiple scales, while accommodating the flexibility in decision making often required by practitioners. The techniques developed may have general application elsewhere. The specific objectives of the research are to:

(1) develop a spatially explicit methodology for identifying and improving connectivity and provide natural resource management agencies with the knowledge base for implementing revegetation actions for maximum biodiversity benefit (Chapter 2).

(2) apply metapopulation theory to a fragmentation-sensitive woodland and forest specialist generic focal species (GFS) and predict landscape capacity, the distribution of persistent GFS populations and their potential dispersal pathways to highlight connectivity gaps between populations (Chapter 3).

(3) gain insight into the relationship between two representations of habitat suitability—indicated by past observations of species and GFS-predicted occupancy—in order to influence restoration actions (Chapter 4).

(4) evaluate recently established revegetation in the study region in relation to two questions: did the design of the revegetated patches conform to aspects known to influence biodiversity response to revegetation, and was revegetation located where it had the potential to contribute greatest benefit to biodiversity? (Chapter 5)?

(5) synthesise results of Chapters 2 to 4 and present conclusions (Chapter 6).

4 Thesis outline

Chapter 2 presents a new methodology for identifying and improving connectivity, aimed at addressing knowledge and extension gaps for two NRM agencies in regional NSW. The methodology encompasses different spatial scales by combining (1) a new, rapid assessment method to evaluate local-scale and regional-scale connectivity with (2) a pre-existing broad-scale mapping of depleted habitats and wildlife corridors at the sub-continental (state) scale. Using habitat configuration, quality and quantity, and generalised estimates of species movement, existing connectivity linkages and gaps across the landscape were identified, which can be targeted for revegetation. The methodology was developed in response to the decision-support needs of the NRM agencies to maintain and restore landscape connectivity across their jurisdictions. A series of spatial products were delivered to the NRM agencies for inclusion in their decision making and investment prioritisation processes.

Chapter 3 introduces an approach to identifying connectivity by applying metapopulation theory to a generic focal species (GFS) consisting of fragmentation-sensitive woodland and forest specialist vertebrates as a surrogate for biodiversity more generally. The approach incorporates

expert estimates of the biogeographic requirements and biological characteristics of the surrogate to evaluate the capacity of a fragmented landscape to enable predicted populations to persist. A novel separate analysis of potential dispersal pathways revealed where current habitat configuration aided or impeded GFS-relevant movement through the landscape matrix. Identifying biogeographic impediments to dispersal can guide the placement of revegetation to link and better sustain these populations.

Chapter 4 evaluates the congruence of predicted GFS occupancy from Chapter 3 and empirical observations of the constituent species to gain an insight into the relationship between two representations of habitat suitability—one indicated by past observations of species and the other being GFS predicted occupancy—in order to influence restoration actions. Detections of the GFS were tested against the predicted occupancy of the GFS using generalised linear modelling. Sensitivity analyses were conducted to improve the congruence between predicted occupancy persistence and observations. Lessons learnt from this approach are discussed, including the difficulty of testing a metapopulation model designed to predict long-term future occupancy and the effect of the quality of the empirical dataset on results and conclusions.

Chapter 5 evaluates revegetation activities conducted in the study region from 2012–2016 from a biodiversity perspective. This was achieved by combining the best-parameterised GFS model from Chapter 4, the state-wide and regional mapping products from Chapter 2, and patch design features known to benefit biodiversity in a qualitative assessment of the plantings to reveal if the works were placed in zones most likely to contribute to improvements in landscape connectivity and persistence of the GFS. Recommendations are made for improving the impact of future revegetation effort on regional biodiversity.

Chapter 6 provides a synthesis of the results of the thesis, summarises the main findings, and discusses the limitations of the research and ideas for future research. A concept model for how the methods derived in this research might be implemented is also presented.

The relationship between each chapter and the envisioned biodiversity outcomes are shown in Fig. 1.

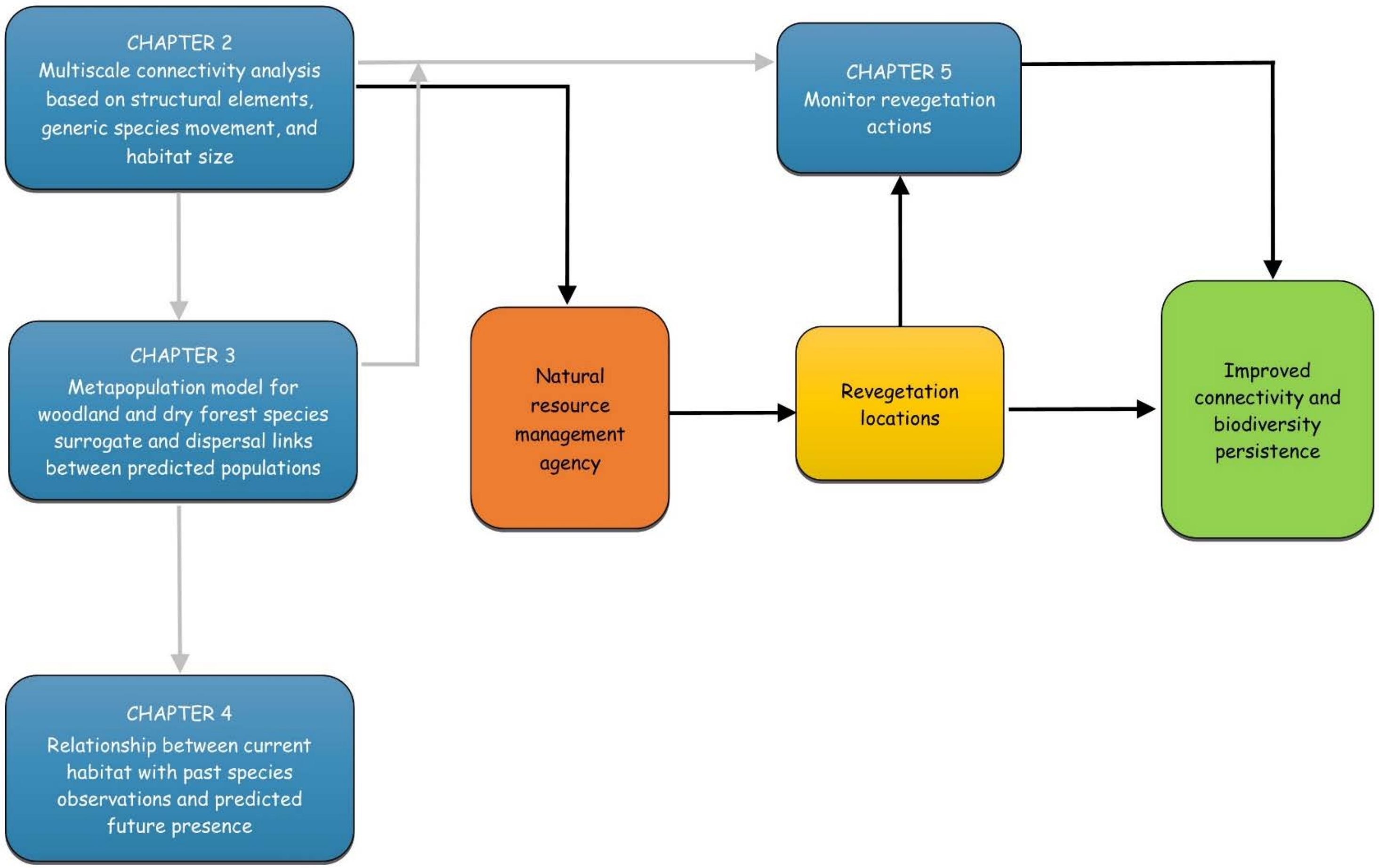

Fig. 1 Schematic representing chapters of the thesis and the connections to an NRM agency and biodiversity outcomes. Black lines represent pathways between chapters and outcome; grey lines represent links between chapters.

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Chapter 4

Validating a forward-looking metapopulation occupancy model using detection data reveals greater than expected disparity in habitat suitability

Abstract

Context Conservation practitioners planning for connectivity restoration need guidance on where to direct actions. Knowing if past capacity of the landscape to support species will continue into the future may assist in decision making.

Objectives We used a model evaluation process to gain insight into the relationship between alternative representations of habitat suitability represented by historical observation and a predictive metapopulation model.

Methods Predicted habitat suitability was derived from a predictive metapopulation model of a woodland generic focal species (GFS) and the occurrence observations of the species comprising the GFS inferred historical habitat suitability. The GFS model was examined through visual overlap of records with predicted occurrence and logistic regression to test the predictive quality of the model. Sensitivity analyses were conducted to improve the fit of the model. We used Border Rivers – Gwydir catchment, eastern New South Wales (NSW), Australia, to demonstrate our approach.

Results Historical GFS observations and predicted future persistent occupancy were not well aligned. Their congruence could not be improved by altering model parameter values in the sensitivity analyses. Comparison of observations of one constituent species and the model

suggest a likely lag effects due to a probable extinction debt. However, results are predicated on incomplete, biased observational records.

Conclusions Based on landscape considerations only, the landscape required for persistence of woodland species differs from that which has supported occupancy. Actions to improve habitat connectivity are therefore required.

Keywords: Evaluation ● REMP ● Metapopulation ● Persistence ● GFS ● Logistic regression ● Planning

Introduction

Predictive models of species occupancy, developed from species distribution models (e.g. habitat models) or population viability analysis (e.g. stochastic patch occupancy models), are frequently used in planning and for a variety of biodiversity conservation objectives. These objectives include reserve selection (Ferrier and Watson 1997; Haight and Travis 2008), threat assessment (e.g. plant invasions, Peterson 2003; or changed fire regimes, Pickens et al. 2017), species management (Lindenmayer and Lacy 1995; Scotts and Drielsma 2003; Weller 2008; Cunningham et al. 2016), predicting extinction (Keith et al. 2008), determining corridors for species movement (Li et al. 2013; de la Torre et al. 2017) and landscape reconstruction and scenario evaluation (Fleishman et al. 2001; Westphal et al. 2003; Aben et al. 2016). Yet uncertainty is an unavoidable part of modelling as all models are imperfect representations of a system, built from incomplete and often biased information (Pearce and Ferrier 2000; McCarthy et al. 2001a). Evaluating a model to estimate it's accuracy and identify its weaknesses assists the model developer to diagnose problems, helps find directions for improvement (Vaughan and Ormerod 2005) and informs end users of the model's fitness for purpose (Pearce et al. 2001).

We set out to evaluate a previously developed predictive metapopulation model that predicted occupancy of a specialist woodland and dry forest generic focal species (GFS) and mapped associated dispersal links, developed from the Rapid Evaluation of Metapopulations (REMP) system and the Spatial Links Tool (Foster et al. 2017). The model was developed to account for multiple species' needs in guiding revegetation efforts to link habitats. The approach incorporated the biogeographic needs and biological characteristics of species sensitive to fragmentation in order to evaluate the capacity of a fragmented landscape to support populations. The GFS is based on a group of ten specialist woodland and dry forest vertebrate species that are sensitive to habitat fragmentation and have limited dispersal abilities (Doerr et al. 2013). REMP is a mechanistic (process-based) modelling system which combines habitat suitability with process-

based entity (species or species group) characteristics (such as estimated dispersal distance and minimum viable habitat size). REMP estimate a region's capacity to support the entity based on landscape structure: the quality, extent and physiognomy of habitat in the region (Dunning et al. 1992; Taylor et al. 1993). A spatially explicit occupancy map and a metric of metapopulation capacity is produced. In this instance, our region was assessed from the perspective of the GFS.

In REMP, the probability that a site will be occupied and the persistence of a population are primarily a reflection of the ability of landscape to support species into the future. It does not fully reflect other ecological considerations (e.g. inter-specific interactions) and non-landscape related threats (Drielsma and Ferrier 2009). REMP is therefore suited to the role of informing conservation actions that seek to conserve or modify landscape structure. The GFS REMP model was applied to the Brigalow–Nandewar Biolinks revegetation project in northern New South Wales, Australia, with the aim of directing revegetation to areas that could facilitate species movement between populations and assist population viability. Henceforth we refer to the GFS REMP model for this region as 'the model'.

REMP parameters, including habitat suitability across a variety of conditions, were previously garnered from expert opinion (Doerr et al. 2013). In the parameter solicitation process, experts were asked to provide values that, all else being equal, would provide a landscape capable of supporting a population in the long term (100 years hence). REMP then provided the framework to render the estimates spatially.

We originally envisaged this study as an evaluation solely of the model's performance, undertaken by comparing the model output against empirical observations. Other research has focussed on testing predictive metapopulation models of a single species (McCarthy et al. 2000; Lindenmayer and Lacy 2002; Nielsen et al. 2008) but not of multiple species or a GFS metapopulation, hence the novelty of our approach. Upon reviewing the progress of the analysis, we reconsidered our aims as it became clear that the original intention was hindered by the fact

that our study area is in transition, having had much of its native vegetation cleared and altered in relatively recent history (from around the middle of the 20th century). The model is forward looking, describing a future equilibrium state arising over time due to the population dynamics set in place by current habitat structure. Empirical occurrence data, on the other hand, is drawn from the recent past, at which point the full impacts of previous disturbances have had insufficient time to fully play out in relation to population dynamics. Therefore, our modelling and evaluation approaches necessarily differ from other model performance literature where empirical occurrence data is used to train the model, followed by evaluation and validation using either an independent test dataset (e.g. Ferrier and Watson 1997; Brook et al. 2000; McCarthy et al. 2001b; Jepsen et al. 2005; Liu et al. 2013) or resampling methods such as bootstrapping or jack-knifing (Vaughan and Ormerod 2005).

Apart from potential lag effects, there were two other potential sources of deviation between the model and the empirical data. The first relates to the discrepancy between parameter values for the composite GFS species and the individual constituent species. The values for each REMP parameter were reduced from 10 individual values to a single value to represent the GFS. This inevitably over-estimated or under-estimated the parameter for at least some of the constituent species. The second source of deviation is related to errors within the combinatorial data reflecting such things as bias in sample locations, errors in recording geospatial locations or misidentification of taxa (Elith et al. 2006; Graham et al. 2008 Fithian et al. 2015). Despite the acknowledged difficulties, such databases have routinely been used by other researchers for development of correlative models (Bennett and Ford 1997; Barrett et al. 2007; Kearney et al. 2010; Roger et al. 2012; Liu et al. 2013). Without conducting our own systematic, long-term surveys, alternative sources of data were not readily available.

For the reasons provided above, it was not possible for us to validate the model in the normal sense. Nevertheless, there is merit in adopting an evaluation approach to: (1) quantify any discord

between the empirical and modelled data; (2) attempt to calibrate the model to reduce the discord, and (3) in light of these, explore the likelihood of a lag effect or other explanations for any discord that may have implications for restoration efforts. The overall aim of the study therefore became: to gain insight into the relationship between two representations of habitat suitability—one indicated by past observations of species and the other being GFS-predicted occupancy—in order to influence restoration actions.

For the purposes of the our evaluation, we assumed the fidelity of the empirical data and notionally tested model performance, and undertook calibration and sensitivity analysis of the occupancy component of the REMP-links model using pooled detection–non-detection data. We obtained the data from a combinatorial database, the NSW Wildlife Atlas (NSW Office of Environment and Heritage).

The term calibration can be defined both as a model property and as a process aimed at model improvement. We use the term in both capacities. As a property, calibration is the agreement between predicted probabilities of occupancy and the observed proportions of sites occupied, and forms part of the evaluation of model performance (Pearce and Ferrier 2000). This has also been termed operational validation as it compares the model against real data and assesses if the model meets a specified performance criterion such as a statistical property like goodness-of-fit (Ryliel 1996). As a process, calibration is a series of modifications of an existing model's parameters with the aim of improving the agreement between predictions and observations (Ryliel 1996; McCarthy and Broome 2000). In this study, model calibration was initially based on expert knowledge followed by a series of manual calibrations to improve discrimination of the model. The degree of manual calibration was determined from a series of sensitivity analyses and subsequent adjustment of the parameter values based on preliminary results (van Vliet et al. 2016). Given the likelihood of lag effects, we do not propose that the calibration necessarily improves the model in respect to predicting future persistence. However, it was of interest

whether the model could be configured to predict 'current' (recent) occupancy spatially, before searching for possible reasons if this was not the case.

The Methods and Results sections describe and present the results of evaluation and calibration analyses, namely (1) the congruence of the model prediction of occupancy with species observations, and (2) determining of how model parameterisation might be altered to improve alignment with species observations. The methods focus on a range of qualitative comparisons of species records with the GFS model and statistical methods correlating the predictive model against known presences and 'pseudo-absences' of the GFS. The Discussion explores model accuracy and improving the model fit and limitations of the methods. In the final section, we present conclusions about the potential difference between habitat suitability related to present occurrence and future persistence.

Methods

Metapopulation models

REMP is a process-based spatial modelling approach that synthesises metapopulation ecology and landscape ecology (Drielsma and Ferrier 2009) and employs a species-focussed approach to assess landscape fragmentation by integrating biological processes with landscape habitat patterns. The GFS took on the role of a 'species' or 'entity' in REMP calculations. The species used to construct the GFS are shown in Table 1. Two alternative parameterisations of the GFS were compared with the observed data (GFS1 and GFS2; Doerr et al. 2013). Estimates of the values for the REMP biological parameters (movement distances, minimum viable habitat area, and habitat suitability under different combinations of land use/vegetation formations) were obtained through a combination of expert solicitation and literature review (Doerr et al. 2013). Values for GFS1 constituted the 25th percentile values for minimum viable habitat area and movement distances of the group. GFS2 constituted 25th percentile values for minimum viable

habitat area and median values for movement distances of the group. The GFS2 was parameterised because Doerr et al. (2013) were concerned the 25th percentile values for movement may have been too unrealistic. That is, maintaining a landscape which was suitable for 75% of species values may have been too ambitious a goal but 50% was considered less so (Doerr et al. 2013). Final parameter values are supplied in Appendix S2 (Table S2).

The GFS is a theoretical species and to investigate how well the GFS represented its constituent species, its predicted occupancy distribution was compared to individual-species occupancy models. Parameter values for the individual species models were derived from expert opinion (E. Doerr pers. com.) and are supplied in Appendix S2 (Table S3).

All spatial inputs were obtained from the NSW Office of Environment and Heritage and data manipulation was carried out using ArcMap 10.2 with 100-m cell resolution projected to GDA94/NSW Lamberts. A full description of the datasets and their compilation is provided in Foster et al. (2017).

Model evaluation and modification

Model evaluation is best achieved by using a range of methods, as a single criterion rarely provides a complete indication of how a multi-parameter model varies from empirical data (McCarthy et al. 2001b; Lindenmayer and Lacy 2002). Accordingly, visual qualitative comparisons between the model predictions and empirical data combined with quantitative statistical tests were used. Empirical data comprised presence records extracted from the NSW Wildlife Atlas (NSW Office of Environment and Heritage). Presence-only records have been used to create species distribution models (e.g. BIOCLIM, HABITAT, DOMAIN, LIVES; Pearce and Boyce 2006; Tsoar et al. 2007), but the inclusion of absences has been shown to produce more accurate distribution models (Ferrier and Watson 1997), reduce bias (Fithian et al. 2015; Ranc et al. 2016), improve discrimination (Smith 2013) and provide better information about

prevalence (Elith et al. 2011). Modelling occupancy is virtually impossible without absence records (Guillera-Arroita et al. 2015). ‘Pseudo-absences’ can be deduced from background sites—sites within the study region which have not been sampled (Phillips et al. 2009). Alternatively, systematic surveys may provide evidence of absences. Taking absences from the detection sites of non-target species, where equal bias in sampling design and technique between the datasets may be assumed, can produce better models than models obtaining pseudo-absences from background areas beyond the presence sites (Ward et al. 2009; Barbet-Massin et al. 2012). True absence, however, is difficult to ascertain as the absence of a species from a site at the time of survey can be due to factors such as seasonality, survey techniques, observer bias and detectability (Pearce et al. 2001; Li and Hilbert 2008; Elith et al. 2011). Consequently, our dataset is more accurately described as a set of records of detection and non-detection than presences and absences.

Detection and non-detection evaluation dataset

The NSW Wildlife Atlas is a repository of opportunistically and systematically collected presence observations. Whilst it is a source of information on species distributions and habitats, such databases are not without inherent biases related to collection techniques or survey location. Without critical assessment, their value for describing or evaluating species distribution is reduced (Elith et al. 2006; Frithian et al. 2015). We extracted all fauna records post-2005 for the study region (NSW Office of Environment and Heritage, extracted 14 May 2015), resulting in 139,749 fauna records. Only systematic, native fauna survey data were retained, which reduced the dataset to 11,276 species records (see Appendix S1 for further details on filtering of records). We assumed consistent collection techniques within and between survey programmes (if not explicitly stated). Each record was given a unique site number based on geographical coordinates (herein referred to as a site) and further categorised according to the date of survey to create a temporal

sites dataset. The data were split into two datasets: GFS species (791 records) and non-GFS species (10,485 records). Multiple GFS species may have been present at a site, consequently the site was reclassified as either GFS species detected (i.e. at least one GFS constituent species detected) or not detected (i.e. no GFS constituent species detected), further reducing the dataset to 1273 records from 917 sites, consisting of 543 GFS detection sites (42.7%) and 730 GFS non-detection sites (57.3%).

Qualitative evaluation

Qualitative evaluation was undertaken in five ways. First, collection bias was explored in a frequency table, with the proportion of detection sites and non-detection sites calculated to reveal potential bias towards preferred vegetation formations and/or land uses. Our examination of sampling bias related to vegetation formation and land use as these were spatial inputs for REMP but collection bias may also have been reflected in geographical location. For example, more records may have been collected along roadsides or other accessible points (Pearce and Boyce 2006; Fie and Yu 2016). Second, the number of GFS detection sites was compared against the predicted probability of occupancy of the base GFS models. The number of detections for each individual constituent species of the GFS was also compared against the predicted probabilities of occupancy of the base GFS models. The assumption was that more detections would occur in the higher range of predicted GFS occupancy and lower detections would correspond to lower occupancy probabilities. If this pattern was exhibited, the GFS model would describe its constituent species. Correlation between predicted occupancy of the GFS and (1) the total number of detections of the GFS, and (2) the number of detections of each individual species was investigated with Spearman's rho. Third, GFS1 and GFS2 predicted occupancy models were visually assessed for alignment with detection and non-detection sites. Correspondence was considered greater for the GFS2 model (see Results), which influenced subsequent evaluation

paths. Fourth, detection records of the individual GFS species were overlain on the GFS2 occupancy maps to highlight the species that contributed to the alignment between predictions and records. Lastly, for species with sufficient records, the co-occurrence of predicted metapopulations of individual species and GFS2 occupancy was investigated in three ways: (1) the common spatial extent of areas predicted to be occupied (expressed as a percentage); (2) the difference in predicted occupancy probabilities for each cell between both models, and (3) grouping predicted occupancy for each model into 11 probability classes or bins (0%, 1–10%, 11–20%, ... , 91–100%) and calculating the percent overlap for each bin. Mapping was conducted in ArcMap 10.1 and calculations were completed using the Spatial Analyst toolbox. The first task was completed by masking the extent of predicted occupancy of GFS2 with the extent of the distribution of the most abundant of the constituent species in the GFS, the brown treecreeper (*Climacteris picumnus*). The second task used the raster calculator to calculate the absolute difference between cell probability values for the species and GFS2 models. The third task was completed using the Tabulate Area function and summing the area for each bin.

Quantitative evaluation

Discrimination and calibration are two attributes of predictive models that are useful for assessing predictive performance. Discrimination is the capacity of a model to distinguish correctly occupied from unoccupied sites, whilst calibration measures the level of agreement between predicted probabilities of occurrence and observed proportions of occupied sites (Pearce and Ferrier 2000**)**. Discrimination was assessed using four different criteria: sensitivity, specificity, the receiver operating curve (ROC) with the area under the curve (AUC), and the true skills statistic (TSS) (Allouche et al. 2006; Freeman and Moisen 2008), all of which are explained below. Discrimination was explored in the first instance by plotting observed values against predicted probability of occurrence. In an accurate model, there is a clear separation of detection

and non-detection sites with little overlap between bins of the histograms for the two groups; the greater the level of overlap, the lower the discrimination ability of the model (Freeman and Moisen 2008). Ideally, the number of non-detections decreases as the predicted probability of occurrences increases, while conversely the number of detections increases as predicted probability increases, producing a bimodal histogram (Freeman and Moisen 2008). Sensitivity (correctly predicted presences = true positives) and specificity (correctly predicted absences = true negatives) indices summarised the proportion of sites for which the observations and predictions agreed. These indices depend on the choice of a threshold value for separating predicted sites into occupied and unoccupied sites. We set the threshold at 0.5 because our aim was to compare, for instance, how well a 0.4 probability of occurrence reflected 40% observed occurrence (Freeman and Moisen 2008). The AUC value from the ROC curve, however, is threshold-independent. It describes the compromises that are made between sensitivity and false positives (incorrectly classifying a site as a detection site, when observational data records non-detection) as the decision threshold is varied (Pearce and Ferrier 2000). A model with no predictive power has an AUC of 0.5 (a 45° line), while a perfect model has an AUC of 1.0. Values of 0.5–0.7 indicate poor discrimination or accuracy (Pearce and Ferrier 2000). The final measure of accuracy, the TSS, was developed as an alternative to Cohen's Kappa value, which has often been used to assess model accuracy (Allouche et al. 2006). Kappa, however, is affected by the proportion of sites at which the target species is detected (called prevalence) whereas the TSS and AUC (Park et al. 2004) are not. Prevalence is the proportion of sites at which the species is recorded as being present, and can bias estimates of accuracy (Allouche et al. 2006). TSS is calculated as Sensitivity + Specificity – 1 and values may range from –1 to +1, where +1 indicates perfect agreement, and values of zero or less indicate that the model performs no better than random (Allouche et al. 2006).

Calibration reflected the reliability of the model to predict that a site would be occupied (e.g. 40% of locations assigned a probability of 0.4 would actually detect a GFS species). To depict model reliability, a calibration (goodness-of-fit) plot was created by plotting observed versus predicted values. A well-calibrated model has all points aligned along a 45° line (Pearce and Ferrier 2000). Sites were firstly grouped into 10 bins based on their predicted values (1–10%, 11–20%, … , 91–100%) and then the bin prevalence (the ratio of sites in each bin with observed values of present versus the total number of sites in the bin) was calculated for each bin. Discrimination indices (except TSS) and calibration plots were calculated using the R PresenceAbsence package (Freeman and Moisen 2008).

A statistical calibration (van Vliet et al. 2016) to determine which model best fit the data was undertaken using logistic regression analysis. Regression analysis can be used to identify significant departures of the points from the 45°diagonal line, suggesting miscalibration of the model (Pearce and Ferrier 2000). A regression line of the logits of the predicted probabilities and the observed proportions was plotted against the untransformed observed and predicted probability axes. This produced a curved line, which described the two components of calibration: bias and spread. Bias is the consistent over-estimation or under-estimation of the probability of occurrence across the entire predicted probability range and is given by the regression intercept. Spread is given by the slope of the regression and describes the systematic departure of the regression line from the diagonal. Significant spread implies that important explanatory variables are missing from the model (Pearce and Ferrier 2000).

The following logistic regression model was used to evaluate model calibration (the relationship between the observed and predicted values):

$$log_e\left[\frac{\hat{\mu}(y)}{1-\hat{\mu}(y)}\right] = \hat{\beta}_0 + \hat{\beta}_1 x \qquad (1)$$

This is the logit link function for a generalised linear model for the Bernoulli variable, y, the observed detection or non-detection of a GFS species, via its probability of success $\mu(y|x)$, where x are the logits of the ten predicted probability classes of occupancy from the model. The intercept, $\hat{\beta}_0$, and slope, $\hat{\beta}_1$, quantify the bias and spread of the model predictions, respectively (Pearce and Ferrier 2000). A perfectly calibrated model would have coefficient value $\hat{\beta}_0$ = 0, indicating no bias, and $\hat{\beta}_1$ = 1, indicating no spread. A significant difference in either coefficient would indicate that the model predictions are significantly different from the observations. The Wald statistic z-test was used to test the two null hypotheses, H_0: $\hat{\beta}_0$ = 0 and H_0: $\hat{\beta}_1$ = 1 (Fox and Weisberg 2011). The logistic regression models were fitted using R (R Core Team 2016).

Qualitative and quantitative analyses were conducted on the GFS1 and GFS2 occupancy models derived from the expert-estimated parameter values. These were referred to as the base models GFS1 and GFS2. As our objective was to see if it was possible to improve alignment between the models and observational data, alternative parameterisations for GFS1 and GFS2 were proposed and the subsequent models evaluated (see below). Regression analysis was conducted on the base GFS1 and GFS2 models, and then only on those alternative models with higher discrimination (AUC value).

Sensitivity analyses and re-calibration

Discrepancies between the predictions of both base GFS1 and GFS2 models with the observational data suggested the models could be improved (see Results). To improve congruence between predictions and observations, we conducted an iterative process of modifying parameters to create a new predictive occupancy model followed by an assessment and evaluation of the results for possible further modification. Three approaches were undertaken: (1) modifying two REMP parameters, minimum viable habitat and movement distances, while retaining base

estimates for habitat suitability (termed behavioural models); (2) varying the expert-estimated habitat suitability ratings while retaining base REMP parameters (termed habitat suitability models), and (3) replacing REMP occupancy probabilities with habitat suitability scores to investigate the role of habitat rather than predicted occupancy (termed habitat predictor models) in achieving alignment with observations.

Seventy-eight new behavioural models were constructed. The three REMP parameters (minimum viable habitat and the movement distances for dispersal and daily foraging) were altered systematically by ±20% for all possible combinations of the three parameters. This produced 52 behavioural models (26 each for GFS1 and GFS2). Subsequent review determined GFS2 provided more promising improvements (greater discrimination capacity as shown by the AUC values, see Results) and additional alternative behavioural models were restricted to GFS2. Further modifications to values, direction of change and parameter combinations were indicated by the AUC of the previous GFS2 model and changes ranged from 30–50%. An additional 26 behavioural models were produced by this procedure.

Twenty habitat suitability models were constructed through two alternative modifications to habitat suitability values. First, values were iteratively downgraded 5–30% across selected combinations of land use and vegetation formations. This process was undertaken for the two most heavily sampled land uses, namely pasture or crops with or without scattered trees, and state reserves. The selected vegetation formations and subformations were the most highly expert-rated formations (100% suitable), the most extensive formations and the most sampled formations. Eighteen alternative habitat models were derived in this manner, with the remaining two of the 20 models derived from varying both REMP parameters and habitat suitability (models GFS2M104 and GFS2M245)). Most models were derived from GFS2 but, for comparative purposes, a limited number was derived from GFS1.

Second, base REMP parameter values were retained but habitat suitability values were downgraded for combinations of vegetation formation and land use, the amount depending on the proportion of detection records. For example, in grassy woodlands in state reserves, a GFS species was detected in 23% of sites, and so the vegetation formation/land use combination was given a 23% habitat suitability score. This was done for both GFS1 and GFS2 (models GFS1M400 and GFS2M400) and resulted in lower estimates of habitat suitability compared to the expert-derived estimates. Values were downgraded from 7–83%, depending on land use and vegetation formation. Manipulating habitat suitability in this manner forced REMP to produce the best fitting model or if improved alignment was not achieved, to highlight shortcomings in either REMP logic or the quality of REMP input data.

Up to this point, predicted occupancy values had been tested against the observational data. The third line of investigation, habitat predictor models, replaced predicted occupancy values with habitat suitability scores. The purpose was to explore the possibility that habitat preferences alone were sufficient to explain the observations, bypassing the need to consider the influence of behavioural processes such as movement distances or minimum viable habitat patch size. Twenty models of this type were developed, the two base habitat parameter models and the 18 alternative habitat parameter models.

In total, 120 models were evaluated using the PresenceAbsence package to determine the model type and variables that best aligned with the observational data and the models to explore further using logistic regression (Appendix S2, Table S5).

Results

Tabular results

The majority of detection and non-detection sites were located in crops and pastures with scattered trees (land use 3) and state protected native ecosystems (land use 9) (Appendix S2,

Table S4). Crops and pastures with scattered trees covered 50.9% of the study region and contained 66.3% of sites with a sampling ratio of 1:3,061. State reserves covered 3.9% of the study region and contributed 15.2% of sites, with a sampling ratio of 1:1,018. The second most extensive land use, crops and pastures without scattered trees (land use 2), covered 41.4% of the catchment but contained only 5.1% of the sites with a sampling ratio of 1:32,339.

Semi-arid woodlands (grassy subformation) was the most extensive vegetation formation occupying 38.8% of the study region and contained the third highest proportion of sites (16.9%) (Appendix S2, Table S4). However, the ratio of number of sites to extent of vegetation formation was the second lowest (1:9,159). Dry sclerophyll forests (shrubby subformation) was the second most extensive formation (22.5%) and contained the second highest proportion of sites (38.4%). The ratio of sites to extent of vegetation formation was at the higher end of the range of values (1:2,340).

There was an increasing trend in detections with increasing probability of occupancy which was more clearly seen in GFS2. Although the correlation between predicted occupancy and number of detections for both the GFS1 and GFS2 models was not significant, the trend was masked by a large number of detection sites in the zero probability of occupancy category (Fig. 1).

GFS distribution maps

Population distribution maps for both parameterisations of the GFS revealed that the broad extent of predicted occupancy coincided with higher estimates of habitat suitability (Appendix S2, Fig. S1). The GFS1 and GFS2 models differed in their respective spatial extents of occupancy and in occurrence probability values; GFS2 predicted greater extent and higher probability of occupancy compared to GFS1. Visual comparison of the distribution of sites against predicted occupancy suggested GFS2 covered more detection sites than GFS1, particularly in the west of

the region (Fig. 2). In both models, there were numerous detection sites in the central zone where no occupancy was predicted and many non-detection sites in the eastern region in areas predicted to be occupied.

Graphical results for individual species

Of the 10 constituent species in the GFS, eight were detected in the region. Records for two species, brush-tailed phascogale (*Phascogale tapoatafa*) and bush stone-curlew (*Burhinus grallarius*), did not meet the criteria used to extract records from the Wildlife Atlas. These records were excluded as they were either opportunistic, detected prior to 2005 or survey methods were ambiguous.

Comparison between individual species detection sites and the two GFS models was possible for brown treecreeper, yellow-footed antechinus (*Antechinus flavipes*), speckled warbler (*Chthonicola sagittata*) and grey-crowned babbler (*Pomatostomus temporalis*) (Fig. 3). Records of the remaining species were too sparse to make useful comparisons. The general trend for brown treecreeper, yellow-footed antechinus and speckled warbler was for more detections in the higher probability ranges with fewer detections at lower probabilities for the GFS2 model. However, brown treecreeper and speckled warbler recorded a high number of detections in the zero probability of occupancy. The trend was less clear with the GFS1 model. Grey-crowned babbler displayed a greater number of detections at a lower probability of occurrence than at higher probability. Yellow-footed antechinus was the only species to record low numbers of detections for zero probability of occurrence and was the only species to show a significant correlation between model prediction and detections (GFS1 model, $r_s = 0.71$, $p < 0.05$; GFS2 model, $r_s = 0.87$, $p < 0.005$).

Distribution maps of individual species

Individual records overlaid on the GFS2 occupancy map showed all but three of the ten species coincided with regions predicted to be occupied (Appendix S2, Fig. S2). These species were barking owl (*Ninox connivens*) (two records dated 2008 and 2012), Boulenger's skink (*Morethia boulengeri*) (one record dated 2012) and grey-crowned babbler (54 records from 33 locations, dated 2006–2013). These aberrant records came from riverine corridors, narrow roadside strips of vegetation or patches smaller than the specified minimum viable habitat size of 1,100 ha.

REMP models for individual species

The most frequently recorded species was the brown treecreeper with 292 records (Table 1). Records of other species were too few to create reliable individual occupancy models. The total area predicted to be occupied by brown treecreeper was 1,258,520 ha compared to the total area of 3,321,375 ha predicted to be occupied by GFS2. Almost the entire brown treecreeper distribution (99.1%) fell within the bounds of GFS2, representing 37.6% of GFS2 extent. The least difference in occupation probabilities between the brown treecreeper and GFS2 models occurred where both models predicted high (>90%) probability of occupancy, and where low GFS2 probability intersected zero predicted occupancy for brown treecreeper (Appendix S2, Fig. S3). Occupancy probabilities grouped into bins of decile ranges showed the brown treecreeper values were similar to the predicted values of GFS2 across 35% of the extent of GFS2 (Table 2). The majority of the convergence between the two models (99.4%) occurred in the 0% bin range, followed by 6.8% convergence for the 91–100% bin range. However, convergence was considerably lower for the remaining categories (1.7%).

Discrimination

Accuracy plots for all models included the distribution of detection and non-detected sites as a function of predicted probability, and the ROC plots with associated AUC values (Fig. 4 and

Appendix S2, Fig. S4). Good discrimination between detection and non-detections should be evident in frequency plots as a clear separation of the two distributions; however, considerable overlap was evident in all models. None of the models produced a typical ROC curve where the curve rises steeply to the upper left corner and then levels off quickly. ROC curves for each of the 120 models closely followed the diagonal line, indicating a near-random discrimination capacity.

The base parameterisation of GFS1 and GFS2 (coded GFS1CU and GFS2CU, respectively) had poor discrimination, evident in the low AUC values (0.584 and 0.593, respectively). Accuracy, as identified by TSS, was also low (0.128 and 0.184, respectively). GFS1CU was better able to predict true absences than true presences (specificity of 0.611 compared to sensitivity of 0.477), but GFS2CU was better able to predict true presences (sensitivity of 0.707 compared to a specificity of 0.517; Appendix S2, Table S5).

The highest AUC values were for two habitat predictor-type models (h_1GFS1M400, 0.633, and h_1GFS2M400, 0.631). This model type replaced predicted occupancy values with habitat suitability (Appendix S2, Table S5) and the habitat suitability parameter values were downgraded proportionally according to the observational data (while maintaining base estimates of minimum viable habitat and movement distances). The index can be interpreted as meaning the model correctly discriminated between detection and non-detection sites only 63.3% of the time, which corroborates the poor discrimination capacity indicated by the ROC curve. Ignoring these two models (which were designed to test the functioning of REMP rather than testing the model with observational data), the models with the highest AUC scores were behavioural-type models. For these models, AUC was improved by keeping minimum viable habitat and forage distances constant but increasing dispersal distance by 30 or 40%. Alternatively, keeping minimum viable habitat and dispersal distances constant but increasing forage distance by 30 or 40% further improved AUC. Lower AUC values (0.538–0.579) were obtained for the remaining habitat

predictor-type models where habitat suitability values were modified without considering the observational data.

The TSS values for all models were greater than zero (indicating the models were better than random) but the highest value of 0.207, for a habitat suitability-type model GFS2M400, was much less than the perfect-fit value of 1 (Appendix S2, Table S5). This model was the result of proportionally downgrading the habitat suitability values according to observational data. The next most accurate model (GFS2M47, 0.206) was the result of increasing minimum viable habitat by 30% while retaining movement distances constant.

Calibration and regression

The goodness-of-fit plot (an indication of level of calibration) depicted the predicted probability of occurrence and the proportion of sites observed to be occupied (Fig. 4 and Appendix S2, Fig. S4). If a model's predicted probabilities are in perfect agreement with observed occurrences, the points of the graph lie along the 45° line. Few of the 120 models depicted such a relationship between predictions and observations, and most points departed from the diagonal. Points fell on the diagonal line more frequently in the lower (10–30%) or mid (40–70% probability) range of predicted values. More often, at predicted probability > 0.5, observed values were below the diagonal line, indicating the model was over-estimating occupancy. When predicted probability was < 0.5, observed values were generally above the diagonal, which indicated under-estimation. This relationship was more evident in GFS1 models (base and alternative parameterisations). The departure of points in calibration plots from the 45° diagonal was tested for significance using logit regressions for 13 models with AUC > 0.6 (Table 3) and a smooth curve fitted to the points (Appendix S2, Fig. S5). Using the base parameterisation of GFS1 (GFS1CU in Table 3) as an example of model results, the change in deviance between the fitted observed model and the null model was 32.74 on 1 degree of freedom ($p < 0.001$). This

indicated the regression curve departed significantly from the diagonal line (Fig. 5), that is, $\hat{\beta}_0$ and/or $\hat{\beta}_1$ differed from 0 and 1, respectively. The Wald's z-test showed that this departure resulted from both significant bias and spread ($p < 0.001$ for both). The bias value $\hat{\beta}_0 < 0$ indicated predicted probabilities of the model were generally too high. The slope value $0 < \hat{\beta}_1 < 1$ pointed to predicted values < 0.5 being under-estimated and those > 0.5 being over-estimated. Similar results were obtained for the remaining 12 of 13 models. The single deviation from this pattern was the bias of GFS1M400 (an alternative parameterisation of GFS1, where habitat suitability was downgraded to reflect observed occurrence). Bias was not significantly different from 0, indicating the intercept was placed at a point where the model did not consistently (along the entire range of probabilities) under-estimate or over-estimate probability of occurrence. Spread, however, remained significant.

Discussion

Understanding how the current landscape is related to future persistence of biodiversity is useful for managers planning conservation actions. We used a GFS derived from fragmentation-sensitive woodland and forest specialist vertebrates to examine the difference in current habitat suitability, represented by empirical observations, with habitat suitable for its predicted metapopulation persistence, represented by predicted occupancy. We found the current observations and predicted occupancy were not well aligned. The reason for this is unclear; however, this result are predicated on incomplete, biased observational records with the potential for a lag effect (extinction debt), making the metapopulation model difficult to test.

Tabular results

Most land uses were well-sampled, but the second most extensive land use, crops without scattered trees, was under-sampled. Cropping areas are assumed to provide little habitat value for wildlife so systematic surveys were biased towards habitats of assumed greater potential. The experts also assumed crops without scattered trees to have low suitability and estimated this land use would provide a maximum of only 25% of a species' habitat resource requirements. However, one of the three formations considered most suitable (100%) by the experts as habitat—semi-arid woodlands (grassy subformation)—was under-represented in the empirical dataset despite being the most extensive vegetation formation.

The quantitative evaluation of the models was expected to be affected by both the unequal representation of detection and non-detection sites within and between most vegetation formations and land uses, and the under-representation of extensive land uses and formations. This was confirmed by a significant bias in the regression analyses but any conclusions relating to the performance of the models are contingent on the quality of the data. A larger dataset may have increased the number of samples in under-represented categories and result in different quality data, producing different assessments of model quality (Rykiel 1996; McCarthy et al. 2001b).

Coincidence of GFS detection/non-detection sites and GFS occupancy

The occupancy models derived by REMP are metapopulation persistence models and not species distribution models. The models describe where a population is likely to persist in the long term under the specified habitat and behavioural parameters. An observational record not coincident with the occupancy extent predicted by a model may represent a vagrant, lingering or dispersing individual of a species rather than a member of a persistent population. The improved alignment of predicted occupancy and observational records of GFS2 over GFS1 was attributed to the less restrictive parameter values of the GFS2 and the assumption of a greater ability of the GFS2 to access habitat. This trend was also seen in the frequency of number of detection sites

against GFS2 probabilities. GFS2 populations will persist because (as defined by REMP) the vegetation formations that are able to provide the required resources are accessible. However, it is not feasible to determine from this qualitative assessment if the model was parameterised well enough to discriminate more clearly between occupied sites and unoccupied sites.

Comparison of single species records with GFS occupancy

The spatial distribution of individual species coincided more generally with the extent of habitat and predicted occupancy of the GFS2 model. However, the detection of species such as the grey-crowned babbler in the highly cleared central zone, where the GFS was predicted to be absent, was a marked departure from the model predictions. The discrepancy can be explained by: (1) the minimum viable habitat patch size (1,100 ha) excluding smaller patches such as narrow riverine corridors and narrow roadside strips of vegetation where babblers were recorded, and (2) recent habitat change (such as habitat removal or reduction), just prior to 2005 (the date of the land use layer), creating a future extinction debt. This debt would see these species extirpated from the landscape sometime in the future, concurring with REMP predictions, but they may persist and continue to be observed in the short term (Tilman et al. 1994; Loehle and Li, 1996; Dullinger et al. 2013; Essl et al. 2015). That is, babbler groups persist for a few years in small habitat remnants but are predicted to shortly become extinct. Another consideration is that resources may have been sufficient only for foraging, or an individual or group may have been dispersing to new territory. REMP predicts metapopulation persistence rather than estimating species range and, as such, some records of constituent species, even in the long term, may not coincide with predicted occupancy.

Individual species REMP model comparison with GFS2

The purpose of comparing a single species model with the GFS2 model was to examine their concordance, based on extent and probability of predictions, and to assess whether management options relevant to the GFS would also be appropriate for managing single species. This avenue could only be partly explored due to the scarcity of data for individual species other than brown treecreeper. The population extent of the brown treecreeper was confined within the extent of the GFS2 predicted population and there was coarse agreement between models for probability values at either end of the spectrum (i.e. at high and zero probability of occupancy). This corresponded with habitat suitability and arrangement of habitat patches. Large patches of contiguous, highly suitable habitat provided accessible resources for both brown treecreeper and the GFS, resulting in the correspondence of higher range probabilities for both models. Differences between the models in the probabilities of occupancy and predicted population distribution were attributable to isolated habitat patches which, while remaining accessible to the wider-ranging GFS2, were inaccessible to the brown treecreeper owing to the species' weaker dispersal ability. Where the brown treecreeper model was confined within the broader GFS2 model, management actions to link GFS2 populations would also potentially benefit brown treecreeper populations. However, in landscapes where GFS2 populations were broadly contiguous, as in the east of the region, there were few opportunities or requirements for linking GFS2 populations. This could be to the detriment of a single species, but fine-scale interrogation of the GFS2 model may find linkages not obvious at broad scales. In landscapes where GFS2 populations were more fragmented, as in the west of the region, there is greater scope for simultaneously linking GFS2 and single species' populations as the coincidence of populations of both entities is clearer. Thus, any plan to improve the persistence of woodland specialists with poor dispersal ability may benefit from a combined approach employing both types of models—the generic group and the single species. The benefit would depend on management goals such as maximising the opportunity for all species in the group or the intersection of all species and single species of the group.

Model modification

Neither good discrimination nor calibration was displayed by either base GFS model (GFS1 or GFS2) or the 11 alternative parameterised models when examined by regression analysis. Calibration bias was present in all models bar one and probabilities were frequently over-estimated and under-estimated. Calibration bias results from differences in prevalence between the model development and test datasets (Pearce and Ferrier 2000) but this was not the case here, as the model was not developed from field data. However, prevalence was low in the observational data (0.428) and this would affect bias. Low prevalence could have arisen due to poor sampling density or non-representative sampling, as discussed previously. Lack of discrimination usually indicates that the explanatory variables in the model—in this case, predicted occupancy—are not strongly associated with species presence (Pearce and Ferrier 2000). Over-dispersion in the regression models also signalled the omission of one or more important explanatory variables, and lack of explanatory variables are known to produce over-estimations (absences erroneously predicted as presences) (Lobo and Tognelli 2011). The omission of variables may also relate to the initial REMP calculations of predicted occupancy, as there are likely to be many factors influencing the persistence of species other than purely landscape considerations.

Best alignment was achieved from the behavioural-type models (ignoring the models designed to test the functioning of REMP; see below), where habitat suitability remained unchanged and movement distances and/or minimum viable habitat were modified. The next best models were habitat suitability-type models and the poorest alignment was achieved by the habitat predictor-type models.

Altering the estimates of habitat suitability for incorporation in the habitat suitability-type models had greater impact on improving discrimination when the suitability of agricultural lands (crops and pasture with or without scattered trees) was substantially increased and the suitability

of state reserves and forests was substantially decreased. Evidence of species using habitats previously considered unfavourable has been found elsewhere (Hiers et al. 2016), but in our region this may also indicate a large extinction debt yet to be paid in agricultural lands. However, no habitat suitability-type model was considered sufficiently discriminate to investigate statistically via regression analysis.

Habitat variables are often used to predict species occupancy distribution (Boscolo and Metzger 2011; Awade et al. 2012; McCune 2016), but replacing the predicted occupancy values with habitat suitability values (i.e. habitat predictor-type models) proved least successful in attaining alignment with observations. Thus, predicted occupancy derived from the integration of habitat suitability with population viability considerations provided comparatively better congruence with observations than static habitat models.

One area of uncertainty related to the programme logic of REMP (Rykiel 1996). Although the logic was not the focus of this study, creating a model using the observational data to guide habitat suitability scores was assumed to provide a better fit between observations and prediction of occupancy, in terms of discrimination and calibration, than any alternative habitat or behaviour model. This assumption was proven in both the base GFS habitat predictor-type models having the greatest specificity, the least calibration bias and greatest ability to discriminate accurately between occupied and unoccupied sites. REMP, therefore, performed as expected although the discrimination and calibration results remained poor.

While acknowledging the poor discrimination statistics and calibration measures for the models, trends in the modification of parameter values could nevertheless be discerned. These trends were seen more clearly in the AUC index than the TSS. In discussing model quality, we chose the AUC index over the TSS, as choice of an evaluation criterion should be driven by the goals of the study, not the statistic (Guisan and Zimmermann 2000), and our goal was to search for patterns from sensitivity analysis. Generally, the higher AUC values were derived from GFS2

models, where base and interim model parameter values were less restrictive than GFS1 alternatives. From the short-term perspective of simple species occurrence rather than population persistence, the experts' assessment of suitable habitat and movement behaviour may have been too restrictive. Species may, in fact, be more adaptable and exist under a wider range of habitat conditions and preferences than presumed (Doerr et al. 2013; Hiers et al. 2016) or at least occupy a wider range of sites at the beginning of metapopulation decline forming part of an extinction debt. Specifically for the GFS2 group of behaviour-type models, increasing either dispersal or foraging distance (not simultaneously) by 30% or 40% and retaining the base estimate of MVH resulted in higher discrimination. However, an increase of 50% in either dispersal or foraging distances did not produce further improvement and, in fact, the improvement was less than observed for the 30% and 40% options, indicating a non-linear relationship between improved discrimination and increasing movement distances.

REMP, however, is about species persistence far into the future, rather than historical species distributions. The lack of agreement between observations and predictions of occupancy seen in all models indicates that, based on landscape considerations only and assuming the validity of the model predictions, the landscape required for persistence differs from that which is currently supporting occupancy.

This lack of agreement points to a fundamental difficulty of using historical data with a forward-looking metapopulation model for model-evaluation purposes. For this approach to be generalised to other regions, further consideration needs to be given to resolving this conundrum. The act of selecting an existing GFS or constructing a local GFS (as discussed below) will also have implications for the results as a GFS proves less generalisable across widely dispersed regions. However, the evaluation framework is applicable to any region and if the historical data/forward-looking model conundrum can be resolved, the evaluation approach should contribute to understanding how species populations will persist or if intervention is required.

Limitations

Our model was derived from attributes which were unobservable in the test data, with the exception of habitat preference. An additional consideration is that the occupancy models are a continuous probability surface which were evaluated with observational point data. In such cases, large amounts of point data may be required (McCarthy and Broome 2000).

Uncertainty exists in the spatial inputs (vegetation condition and land use) required by REMP. Spatial data are recognised as inherently containing errors that consequently affect the determination of landscape pattern (Lechner et al. 2012). These errors can arise from the digitising process (e.g. delineation of vegetation formations) and the qualification of attribute data (e.g. misclassification of land use). Land use is also a coarse surrogate for vegetation condition and discrepancies between the coded land use and assumed condition could be encountered at the site level. These uncertainties play out in the determination of occupancy probabilities and model evaluation.

AUC is not only affected by bias but also by low numbers of non-detections, and a larger, more spatially comprehensive dataset may have produced different AUC results. A minimum ratio of 1:100 for detection to non-detection records has been suggested (Lobo and Tognelli 2011) which is a higher ratio than our data of 1:13. If more, evenly distributed ‘pseudo-absences’ from unsuitable habitats had been available for inclusion in our analysis, there may have been higher agreement with zero predicted occupancy.

The GFS was expected to replicate the constituent species but reducing 10 values into a single value for each parameter would have contributed to the poor alignment. Inevitably, the values for some species would have been under-valued or over-valued blurring the congruence between species observations and predictions of occupancy. Although each species that comprised the GFS are considered sensitive to fragmentation, the group was appropriated from another woodland region of NSW. Constructing a GFS from species local to the study region may have

revealed additional or replacement fragmentation-sensitive species. Such a review may have provided a more substantial observational dataset with which to examine the model. This does not discredit the GFS approach, but highlights the need for critical use of existing surrogates when the planning objective of employing a target group of species is to benefit a wider range of species. There may also be value in considering the inclusion (or exclusion) of species which display time-related responses to land-cover changes. Species sensitive or insensitive to time lags may influence the predicted outcomes and management conclusions. It is recommended that a GFS be constructed anew for each region where this approach is implemented.

Irrespective of the qualifications we have placed on the evaluation, the sensitivity analysis indicated greater dispersal distances and greater adaptability of the GFS across differing habitat conditions than estimated by the experts. If regionally the GFS can move further and tolerate habitat that was assumed less optimal, the GFS may not be as sensitive to fragmented habitat in our study region as initially suspected. This assertion may be more relevant in the east rather than the west of the region, the east having more contiguous habitat. Alternatively, the discrepancy between expert's estimates and the empirical data may simply be a manifestation of the pending extinction debt, as GFS populations attempt to modify their activities in order to survive in suboptimal fragmented habitat. This reasoning would apply more in the fragmented west and central regions. A more conclusive alignment may be achieved by separating the region into two geographic subregions and conducting separate evaluations.

The evaluation was largely limited to empirical data collected from areas the model perceived to be of medium to high habitat quality. The most extremely modified parts of the region, places where the model would most likely agree with empirical data, were effectively excluded from the evaluation, which would largely account for the 'poor' alignment between the two. The analysis would have benefited from a larger, more systematic dataset, collected from unsuitable as well as suitable habitat and, if possible, including longitudinal studies (Barnes et al. 2014). However,

complete and reliable field data on species is difficult and expensive to acquire, so critical use of available data is required.

Conclusions

Our objective was to gain insight into the relationship between the two representations of habitat suitability—indicated by past observations of species and GFS predicted occupancy—in order to influence restoration actions. We found that the two representations of habitat suitability were not closely aligned and although the analysis was not definitive, we conclude they provide differing perspectives of habitat use. This conclusion, however, is confounded by the demonstrated bias in the observation data. The indications are that habitat suitable for supporting current occupancy and future long-term occupancy are distinct. This would suggest the likelihood of a regional extinction debt, with grey-crowned babbler, in the central part of the study region, being the most obvious indication of this looming event. Such revelations indicate opportunities for high impact remedial actions (such as revegetation to reconnect habitat), as these actions are could arrest imminent extinctions.

The potential existence of the lag effect between land use change and species response in our study region could be explored by two alternative means. Firstly, a similar analysis could be conducted in another region where the lag effects of past land cover change have had more time to take effect. As more of the extinction debt is likely to have been paid in such a region, we hypothesise that the predictions of the model would better align with observations. Secondly, if comparative spatial data on land use (past and present) are available for our study region, an extinction debt analysis may be conducted to support our suggestion.

Finally, two avenues have emerged as options for improving the analyses. In place of historical observations as a surrogate for habitat, a habitat suitability surface could be derived from the observational data, that is, from a species distribution model. This could then be

compared directly with the suitability surface from REMP to deduce the long-term potential for occupancy. Alternatively, both perspectives of habitat suitability could be combined where the externally derived habitat suitability surface is entered into REMP as the required vegetation condition input.

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Table 1 Species that comprised the woodland and dry forest generic focal species group (from Doerr et al. 2013) and the number of detection sites for each species. More than one species may occur at a site. Detection site = at least one GFS constituent species detected at site

Common name	Specific name	Number of (geographic) sites where detected
Barking owl	*Ninox connivens*	14 sites (14 detections)
Boulenger's Skink	*Morethia boulengeri*	31 sites (42 detections)
Brown treecreeper	*Climacteris picumnus*	189 sites (292 detections)
Brush-tailed phascogale	*Phascogale tapoatafa*	0 sites (0 detections)
Bush stone-curlew	*Burhinus grallarius*	0 sites (0 detections)
Grey-crowned babbler	*Pomatostomus temporalis*	89 sites (157 detections)
Hooded robin	*Melanodryas cucullata*	39 sites (45 detections)
Speckled warbler	*Chthonicola sagittata*	86 sites (177 detections)
Squirrel glider	*Petaurus norfolcensis*	8 sites (8 detections)
Yellow-footed antechinus	*Antechinus flavipes*	32 sites (56 detections)

Table 2 Occupancy (ha) for GFS2 and single species model, brown treecreeper (*Climacteris picumnus*), for each GFS2 occupancy range

Bin range of predicted occupancy (%)	GFS2 occupancy (ha)	Brown treecreeper occupancy (ha)	Spatial overlap (%)
0	1,719,464	1,708,605	99.368
1–10	614,193	101	0.016
11–20	207,863	11	0.005
21–30	152,362	3	0.002
31–40	144,309	7	0.005
41–50	153,456	21	0.014
51–60	169,470	53	0.031
61–70	206,432	52	0.025
71–80	293,679	347	0.118
81–90	635,032	4,261	0.671
91–100	744,579	50,955	6.843
Total (ha)	5,040,839	1,764,416	35.000

Table 3 Estimate of coefficients from logistic regression. All models began with a null deviance of 1744 with 1 degree of freedom. All models had AUC > 0.6 and are listed in order of increasing AUC value. Maximum AUC = 0.633

Model	Bias (intercept)	*z* value and Pr > |*z*|	Spread (slope)	*z* value	Change in deviance with Pr > (Chi)	Change in Df
GFS1CU	-0.199	-3.368 ***	0.156	-30.60 ***	32.74 ***	1
GFS2CU	-0.34	-5.829 ***	0.15	-35.45 ***	40.72 ***	1
GFS2M32	-0.385	-6.424 ***	0.151	-36.70 ***	44.46 ***	1
GFS1M400	-0.087	-1.314	0.178	-26.34 ***	33.20 ***	1
GFS2M92	-0.385	-6.421 ***	0.153	-36.59 ***	45.46 ***	1
GFS2M245	-0.5	-7.474 ***	0.168	-33.77 ***	49.75 ***	1
GFS2M45	-0.511	-7.51 ***	0.167	-33.33 ***	47.86 ***	1

GFS2M72	-0.367	-6.201 ***	0.148	-35.63 ***	39.53 ***	1
GFS2M81	-0.38	-6.352 ***	0.149	-35.44 ***	39.71 ***	1
GFS2M74	-0.354	-6.022 ***	0.14	-36.34 ***	36.37 ***	1
GFS2M83	-0.354	-6.03 ***	0.146	-35.97 ***	39.04 ***	1
h_1GFS2M400	-0.155	-2.596 ***	0.344	-13.26 ***	53.21 ***	1
h_1GFS2M400	-0.125	-2.07 **	0.3849	-12.01 ***	62.73 ***	1

* $p \leq 0.01$, ** $p \leq 0.001$, *** $p \leq 0.000$

Figure captions

Fig. 1 Frequency of detections sites across predicted probabilities of occupancy (10% bins) for the base REMP models GFS1 and GFS2. Detection site = at least one GFS constituent species detected; not detected = no GFS constituent species detected

Fig. 2 Predicted metapopulation occupancy and detection and non-detection sites for base REMP models GFS1 and GFS2. Detection site = at least one GFS constituent species detected; not detected = no GFS constituent species detected

Fig. 3 Frequency of detections for most detected individual species of the GFS across predicted probabilities of occupancy (10% bins) for the base REMP models GFS1 and GFS2

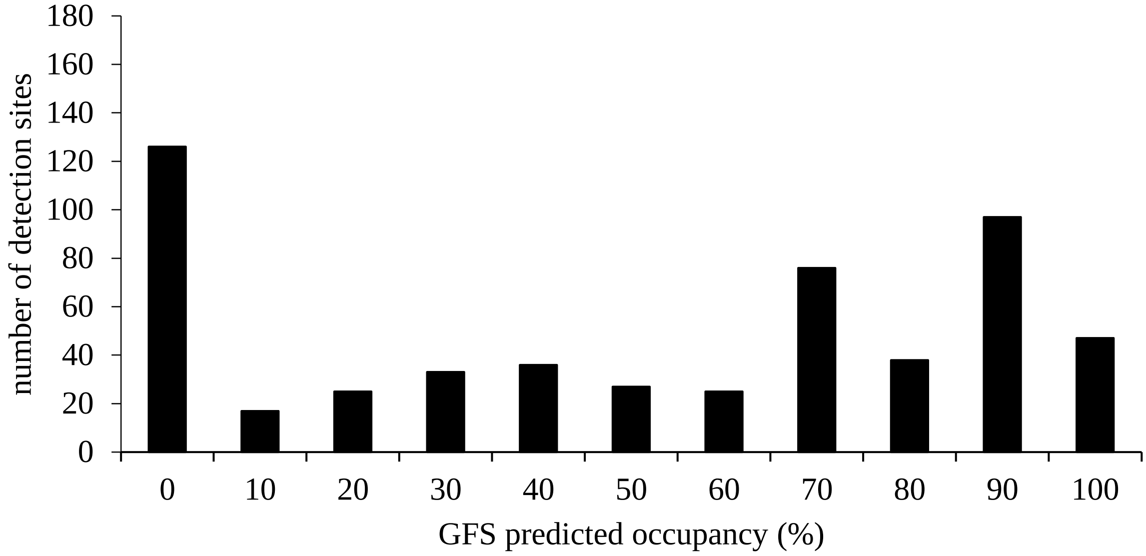
Fig. 4 Accuracy plots for predictive metapopulation occupancy model GFS2 (base model). Histogram (top left) displays the number of presence (GFS species detected) and absence (GFS species not detected) sites against predicted probability of occurrence; the ROC curve and AUC index (bottom left); and calibration plot (predicted occurrence and observed proportion of sites with presences for each bin) with confidence intervals and total number of sites per bin (top right). Accuracy plots were created for all 120 models

Fig. 5 Regression line describing overall relationship between observed and predicted values. Model shown is base parameter values for GFS2 (coded f01CU). The shape of the line describes

over-estimation (under the line) or under-estimation (above the line) of the predictions.

Regression plots were created for 13 models with AUC > 0.6

(a) GFS1



(b) GFS2

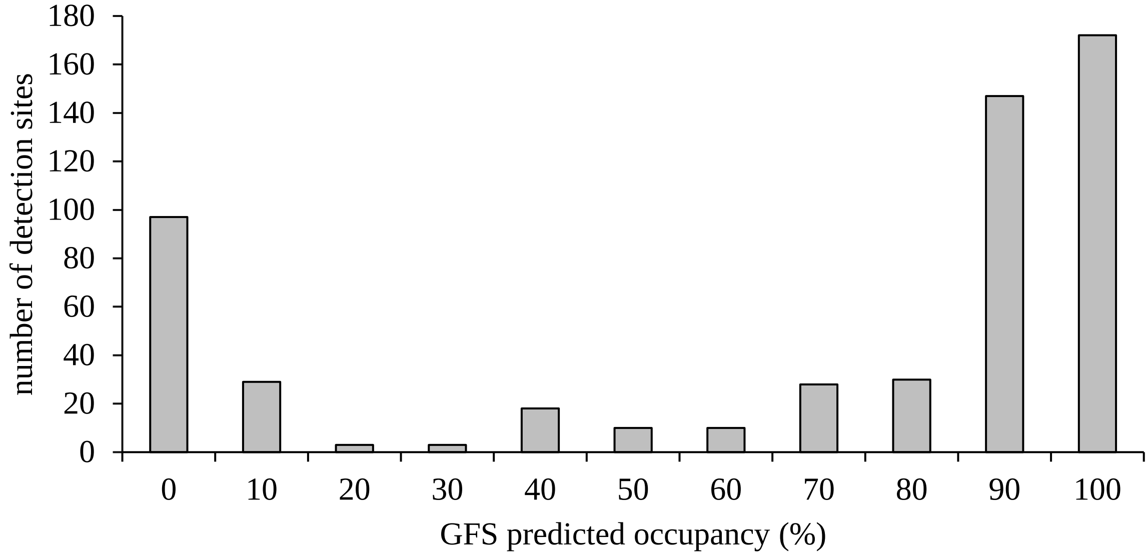


Fig. 1

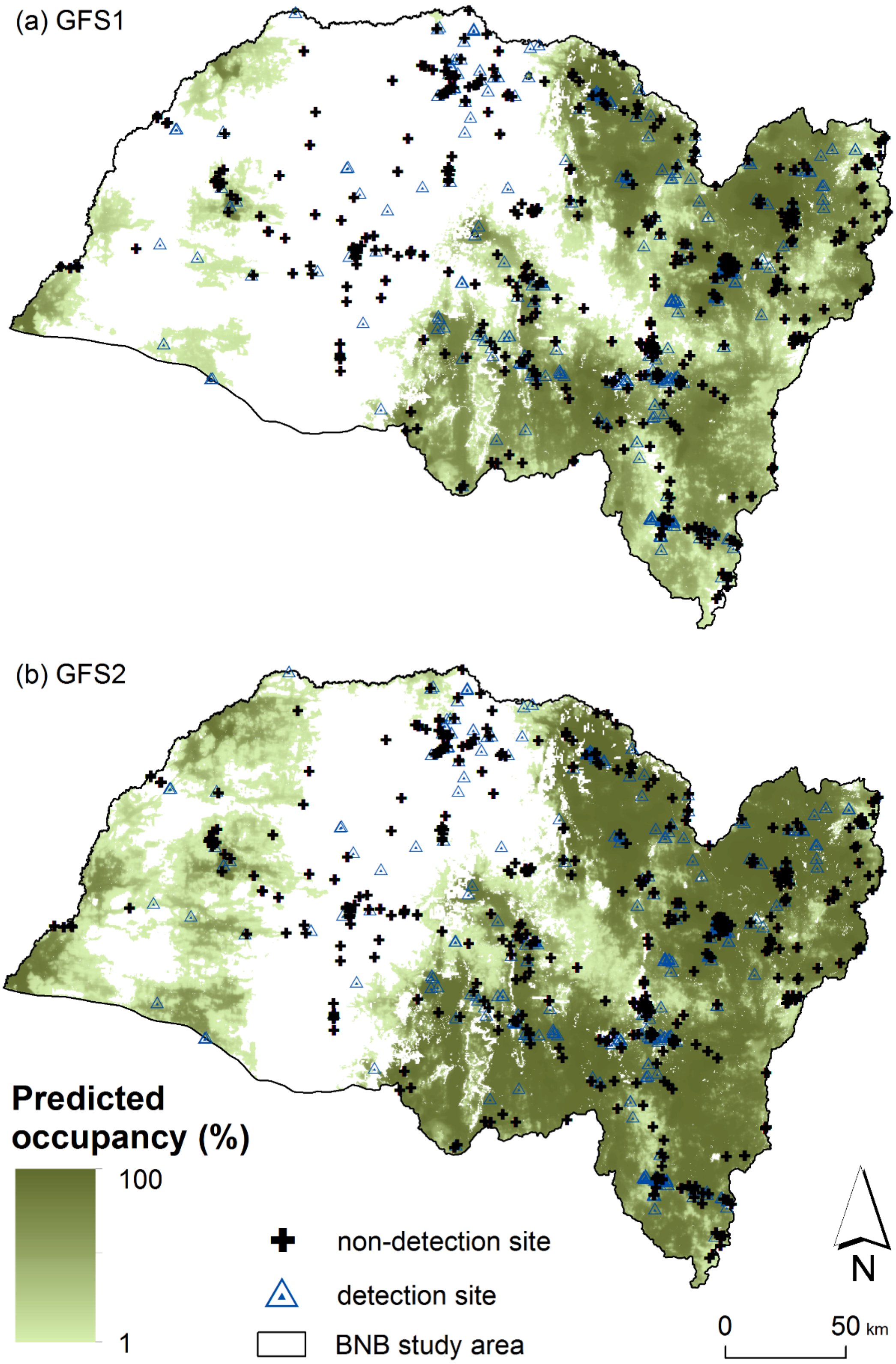
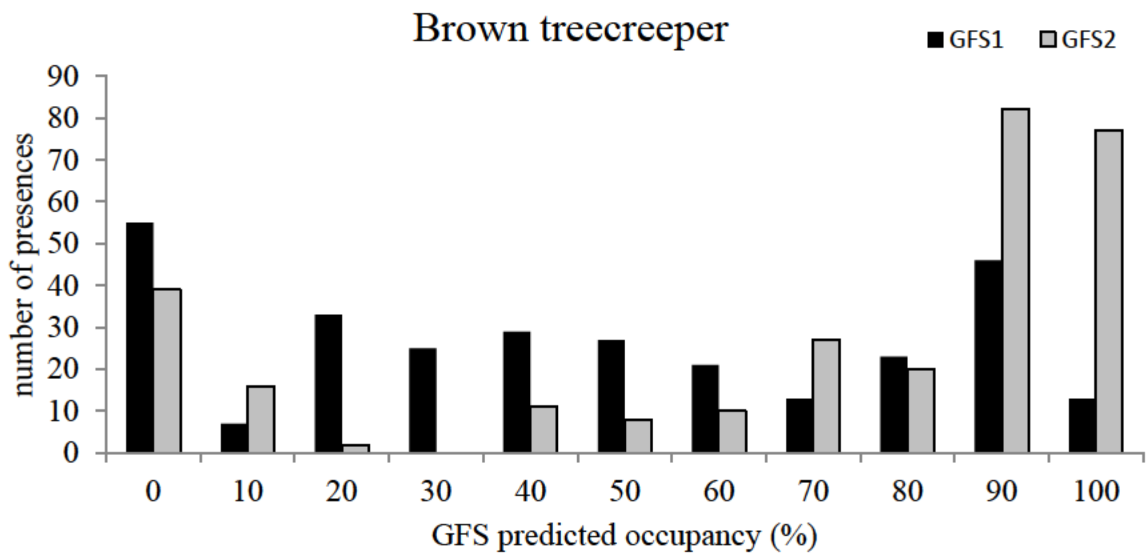
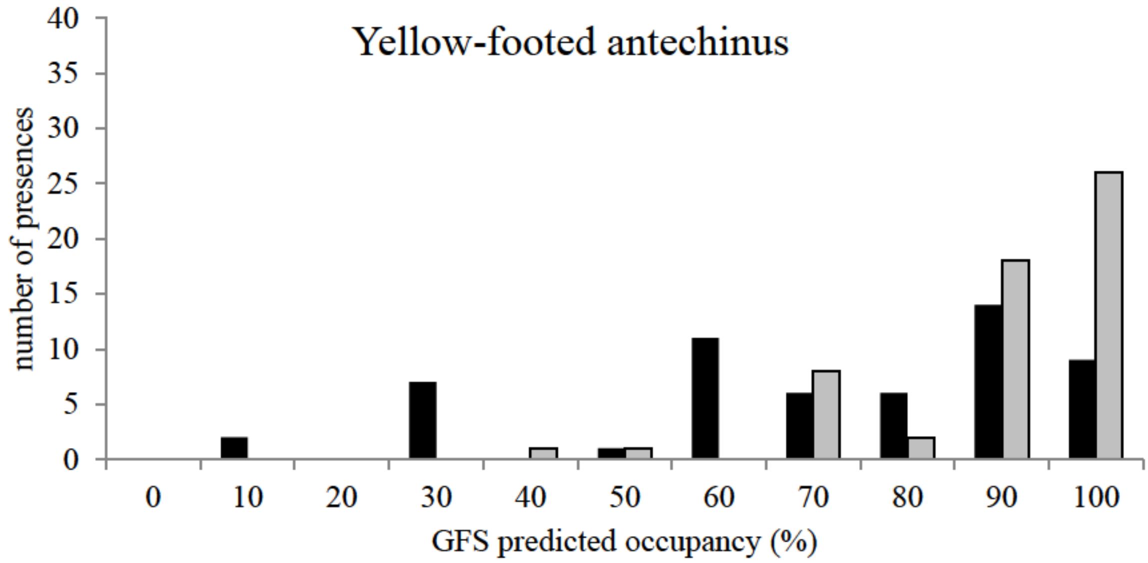
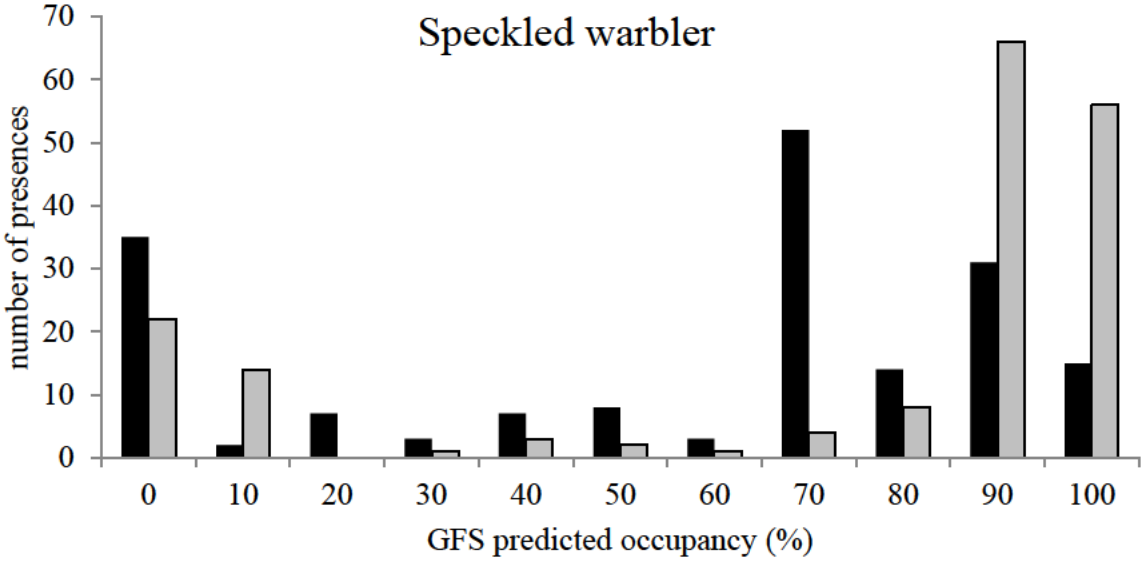

(a) GFS1
(b) GFS2
Predicted occupancy (%)
100
1
non-detection site
detection site
BNB study area
N
0
50 km

Fig. 2


Brown treecreeper
GFS1
GFS2
number of presences
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
80
90
100
GFS predicted occupancy (%)


Yellow-footed antechinus
number of presences
40
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
100
GFS predicted occupancy (%)


Speckled warbler
number of presences
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
80
90
100
GFS predicted occupancy (%)

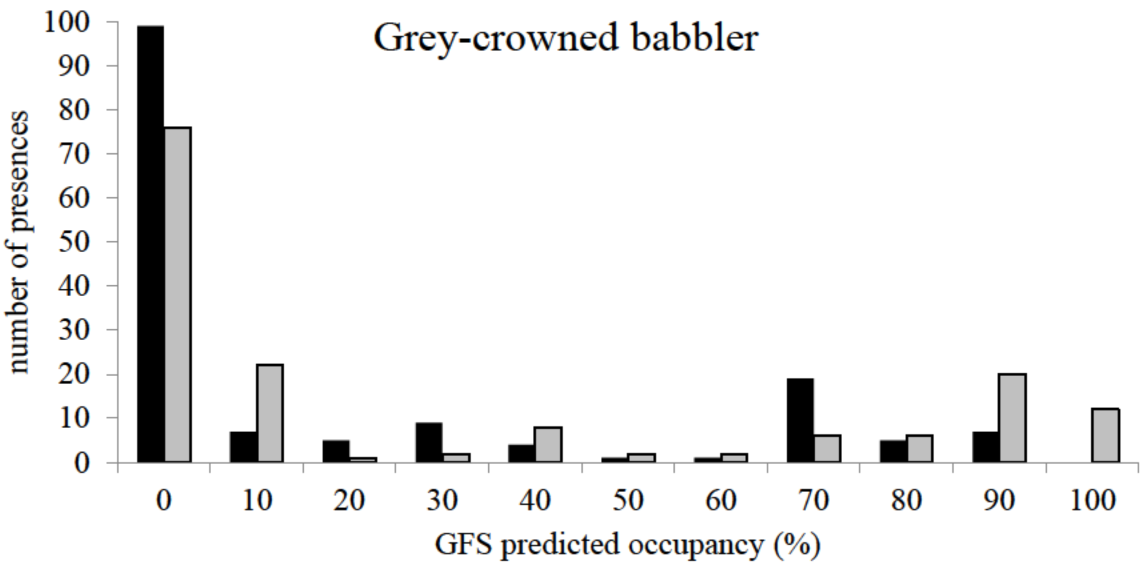

Grey-crowned babbler
number of presences
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
80
90
100
GFS predicted occupancy (%)

Fig. 3

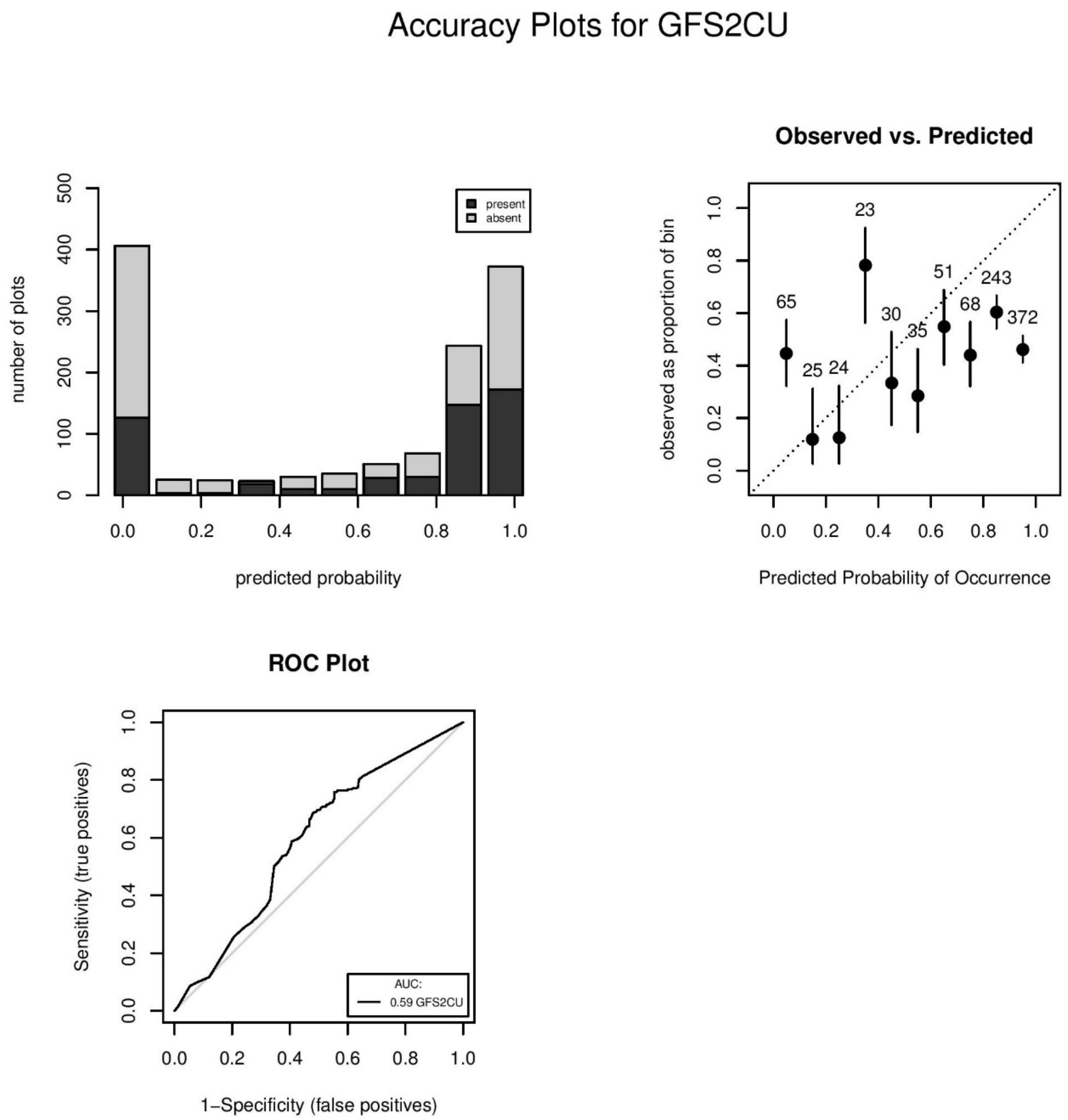

Accuracy Plots for GFS2CU
number of plots
0
100
200
300
400
500
present
absent
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
23
65
51
243
30
35
68
372
25 24
0.0
0.2
0.4
0.6
0.8
1.0
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.59 GFS2CU
1−Specificity (false positives)

Fig. 4

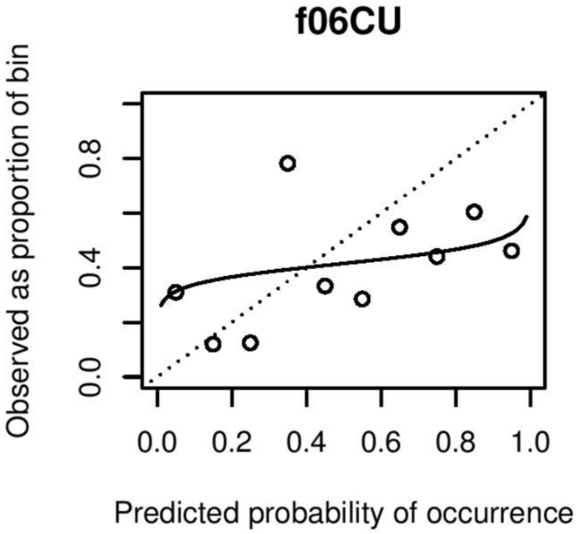

f06CU
Observed as proportion of bin
0.0
0.4
0.8
0.0
0.2
0.4
0.6
0.8
1.0
Predicted probability of occurrence

Fig. 5

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Chapter 5

How effective are local revegetation programmes in conserving biodiversity in fragmented landscapes?

Abstract

Context Remnant native vegetation in agricultural landscapes is often limited to small patches, affecting habitat connectivity, leading to reduced species richness. Connectivity restoration programmes have been initiated widely but reporting on their performance is uncommon and there are no standardised measures of success.

Objectives Our objective was to demonstrate a novel evaluation method, focussing on a metapopulation perspective. We retrospectively assessed a local revegetation programme, asking: (1) did the design of the revegetated patches conform to aspects known to influence biodiversity response to revegetation, and (2) was revegetation located where it had the potential to contribute greatest benefit to biodiversity? We used the revegetation programmes of the Brigalow–Nandewar Biolinks project, eastern New South Wales (NSW), Australia, to demonstrate our approach.

Methods We utilised existing multi-scale connectivity and biodiversity benefits outputs, a metapopulation model for a woodland generic focal species and simple structural metrics to evaluate the cumulative landscape-scale potential benefits from individual plantings. Evaluation assumed greatest biodiversity benefit would arise from plantings located in the intermediate range of the spatial assessment themes and from larger patches close to neighbouring remnants.

Results Plantings were dominated by small patches with high area–edge ratios but none were beyond the maximal distance for dispersal of woodland birds and mammals. Most sites were

within the distance for daily forays. The majority of revegetation was located within high priority zones for revegetation but substantial amounts were established where it was predicted to have minimal long-term potential for improving regional biodiversity. Much additional restoration work would be required to make gains in landscape connectivity and species occurrence and persistence.

Conclusions Our method has demonstrated the use of multi-scale spatial outputs combined with simple structural metrics in evaluating the landscape-scale effects local revegetation programmes. These features could be considered by other researchers wishing to evaluate other local programmes.

Keywords: Evaluation ● Connectivity ● Generic Focal Species ● Native Vegetation Benefits Mapping ● REMP ● Metapopulations

Introduction

Agriculture is a major contributor to the on-going clearing and degradation of habitat, which poses a substantial global threat to biodiversity (McIntyre and Hobbs 1999; MEA 2005; Tilman et al. 2011, ASE 2016). However, biodiversity conservation strategies must include the contributions of both reserved and farmed lands for effective long-term outcomes (Margules and Pressey 2000; Baudron and Giller 2014) but conservation action in agricultural areas present key challenges (Green et al. 2005; Ansell et al. 2016c; Drielsma et al. 2016). This is particularly pertinent in Australia where approximately 13% of threatened species and 21% of critically endangered species are not protected in reserves (Watson et al. 2011) and where clearing of remnant habitat patches and scattered paddock trees for farming continues despite the known detrimental impacts to biodiversity (Bennett and Mac Nally 2004; Donald and Evans 2006; Fischer at al. 2010). Approximately half of Australia's original extent of woody vegetation has been cleared, resulting in declines in both biodiversity and the provision of ecosystem services (Ansell et al. 2016c).

Remnant native vegetation in agricultural landscapes is often limited to small patches, riparian strips, linear stretches along roadsides and scattered paddock trees with the quality of the remnant influenced by the surrounding agricultural practices (Law et al. 2000; Bennett and Mac Nally 2004). Fragmented and degraded habitat creates a patchwork of vegetation set in a matrix of agricultural activities and infrastructure, affecting habitat connectivity for native species (Norton and Reid 2013). This can lead to reduced native species richness and the replacement of species of higher conservation concern with species of lower conservation concern (Donald and Evans 2006). In response to declines in species and ecosystems services, organisations have initiated individual and multi-tenure restoration programmes to improve paddock-scale and landscape-scale connectivity (Soulé et al. 2004; Fitzsimons et al. 2013; Worboys and Pulsford 2011, Whitten et al. 2011). Restoration is an endeavour undertaken for a variety of motivations and incorporates

a range of approaches, techniques and technologies (Suding 2011; Perring et al. 2015). Revegetation is one such approach, implemented for conservation, production or community engagement reasons (Perring et al. 2015; Fifield 2016), where conservation revegetation is undertaken to recreate habitat, improve connectivity or enhance ecosystem functioning (Bennett and Mac Nally 2004; Donald and Evans 2006).

Any restoration activity, however, requires evaluation to document progress and inform adaptive management strategies (Hobbs and Norton 1996). Globally, evidence of restoration progress is rare (Suding 2011; Nilsson et al. 2016). Reporting on performance and expected benefits of undertakings in Australia is similarly uncommon (Duncan and Reich 2016). One explanation could be that the elements of success can be difficult to define and measure (Suding 2011; Wortley et al. 2013). Alternatively, evaluation may occur in an informal context; that is, observations, discussions or thinking occurs, which result in no formal documentation or empirical analysis but may produce modifications to the project. Additionally, documentation, if produced, may form part of grey literature and remain unavailable to other restoration practitioners (Nilsson et al. 2016).

In Australia, state-administered natural resource management (NRM) agencies undertake restoration and conservation planning (Robins and Dovers 2007), aiming to deliver regional-scale outcomes through actions implemented by individual landholders at the farm scale (Zerger et al. 2011). These outcomes are often phrased in terms of targets (Zerger et al. 2009), such as hectares of activity achieved. The pure attainment of targets, however, can become a numerical exercise, independent of any ecological outcomes that may (or may not) arise (Jørgensen 2015) and underscores the necessity of planning, and for determining meaningful measures of restoration success and their reporting.

Three types of attributes are generally reported in restoration evaluation: species diversity and abundance, vegetation structure and ecological functioning (Wortley et al. 2013). For example,

reptiles colonising revegetation patches (Shoo et al. 2014), reduced reptile and arboreal mammal abundance in revegetation compared to remnants (Cunningham et al. 2007), greater macropore density in revegetated sites compared to pastures (Colloff et al. 2010); differing bird responses to revegetation of differing structure (Munro et al. 2011) and reduced presence of arboreal mammals corresponding to reduced vegetation structure in plantings (Lindenmayer et al. 2016). In a departure from site-based attribute assessments, systematic conservation planning has been utilised to evaluate plantings as a network, examining their collective effect on temporal species occurrence at the landscape scale (Ikin et al. 2016). This work highlighted the significance of attributes such as patch size and landscape context for species occurrence.

The Northern Tablelands Local Lands Services and North West Local Land Services (LLS) NRM agencies are responsible for implementing revegetation and other restoration actions in the Border Rivers – Gwydir (BRG) catchment of north-eastern New South Wales (NSW), Australia. The primary objective of each revegetation action may not be improved biodiversity or landscape capacity—soil stability or establishing shelter belts, for instance—and there are also likely private benefits to the landholder for establishing revegetation (Ansell et al. 2016b; Fifield 2016). However, revegetation located anywhere in the landscape may provide a benefit to biodiversity (Hobbs 1993). We conducted an ex post investigation into biodiversity-related benefits of past revegetation actions implemented by the LLSs in the BRG. We chose a novel method to examine biodiversity benefit, focussing on a metapopulation perspective to compare revegetation locations against a series of existing, cross-scale spatial modelling outputs. The effect of revegetation analysed from the perspective of species behaviour and processes such as dispersal, rather than one of evolving species composition or structural change within revegetation patches (Law and Chidel 2006; Munro et al. 2011; Hawes 2016) places species persistence at the epicentre of evaluating landscape change. Biological processes such as dispersal occur across multiple scales (Cadotte and Fukami 2005) and the magnitude of environmental change—in this case, land

clearance—requires a landscape perspective to evaluate restoration (Bell et al. 1997; Perring et al. 2015). For these reasons, we combined all revegetation actions into a single evaluation dataset.

As there is no conclusive measure of restoration success (Suding 2011), we framed our assessment around two research questions: (1) did the design of the revegetated patches conform to aspects known to influence biodiversity response to revegetation, and (2) was revegetation located where it had the potential to contribute greatest benefit to biodiversity? Features known to influence species response include patch size, patch perimeter length and proximity to remnant vegetation (Ansell et al. 2016a). Biodiversity benefit was examined through the lens of existing modelling outputs which included the Native Vegetation Management Benefits mapping (Drielsma et al. 2013) and a regional dispersal pathways analysis (Foster et al. 2016). These were supplemented by predictions of landscape capacity and metapopulation occupancy of a woodland generic focal species group (Foster et al. 2017b), the group being used as a surrogate for fragmentation-sensitive species and general biodiversity. The answers to our research questions will provide specific guidance to the LLSs on the biodiversity outcomes of their investment and demonstrate the role evaluation should play in any restoration project.

Methods

Study region

The natural vegetation of the Border Rivers – Gwydir catchment study region grades from humid high-altitude tableland forest in the east on top of the Great Dividing Range, through open-forest and woodland on the North-West Slopes of NSW in the central catchment, to low-elevation semi-arid open woodland, tall shrubland and grassy plains in the west. The regional economy is based around agriculture (grazing, dryland and irrigated cropping) and rural and regional services. The vegetation has been extensively cleared and modified. Since European arrival, some 71% of the region's native vegetation has been transformed or altered through land use and management

(DECC 2010), resulting in fragmented and variegated landscapes. Woodlands, particularly grassy woodlands, are among the most cleared and modified communities in Australia, resulting in major biodiversity loss (Keith 2004). For example, over one third of Australia's land birds are woodland-dependent but due to habitat clearance and modification, at least one in five of these species are threatened (Birds Australia 2015).

Spatial data

Spatial information relating to on-ground actions for the period 2012–2016 was extracted in September 2016 from the NSW Land Management Database (LMDB), based on the criterion Legend = 'Establish Vegetation'. The LMDB spatially records and describes natural resources management investment, linking business and contract management systems, and tracks funded, on-ground activities (http://lmdb.nrmoptions.nsw.gov.au). The extracted records represented a combination of revegetation sites undertaken as part of the Brigalow–Nandewar Biolinks (BNB) Project and other land management programmes such as soil management (L. Blair pers. comm.). Data cleaning, designed to remove unsuitable, incomplete and/or inaccurate records, is an essential requirement for reliable use of centralised databases (Gueta and Carmel 2016). We applied several cleaning criteria to the data. Confirmation the work had been both implemented (rather than planned) and had the potential to improve biodiversity (i.e. unrelated activities such as pasture cropping were not included) was obtained from the LLSs. Works were excluded if associated information was incomplete (e.g. an omitted contract number). Polygons arising from spatial mapping errors (e.g. topological errors arising from operator error during digitising) were identified and the polygon removed. The final data set consisted of 216 records and represented riparian revegetation, the creation of new patches or linear strips across cleared farmland, linear corridors linking existing remnants, widening of roadside vegetation or the establishment of shelterbelts near or surrounding watering points (e.g. dams). The data was converted to a fine-

grained raster (2 m resolution) in recognition of the small size of the polygons. All data preparation and manipulation was conducted in Arc Map 10.1, with data projected in GDA 1994 Lamberts.

Sites were evaluated as a group rather than individually as a significant number of the LLS sites were considerably smaller than the minimum habitat patch size of 5–15 ha required in woodland and forest systems (Freudenberger 1999; Crossman and Bryan 2006; Huggett 2005).

Vegetation cover information was sourced from existing woody canopy spatial data. The woody canopy was derived from remotely sensed, foliage projective cover (Danaher 2011), constructed from SPOT-5 imagery at 5-m resolution. The layer was re-sampled to 100-m resolution to represent woody cover, irrespective of vegetation type or condition (Roff, unpub.).

Analysis

Studies point towards the importance of patch descriptors (size, distance to next patch and edge–area ratios) as indicators of structural diversity for species. The descriptors are relatively easily understood metrics but give no indication of functional connectivity because they do not incorporate dispersal data. The REMP and the cross-scale network analysis fill the conceptual gap by linking structural characteristics with dispersal estimates and minimum viable habitat size in a regional analysis. The approach is outlined in Fig. 1. Note that a new REMP and network analysis was not conducted using the updated land use layer as the new plantings were considered of insufficient extent to effect regional-scale changes to biodiversity outcomes, although they may affect local-scale changes.

Examining patch design

Patch size, perimeter, width and vicinity to remnant woodland were calculated for each patch. Research has demonstrated smaller patch size and higher area–edge ratios have a negative effect

on species richness (Helzer and Jelinski 1999; Munro et al. 2011). The area–edge ratio gives an indication of the patch geometry, with larger areas and more circular shapes resulting in higher ratios, and smaller and more linear shapes resulting in lower ratios (Smith 2008). We compared the area–edge ratio of a 1-ha circle (the shape with the highest ratio) with the ratio of each revegetation patch. Guidelines for dimensions of revegetation patches suggest large and wide patches are more beneficial for fauna (Munro et al. 2007). In woodland environments, a minimum patch size of 10 ha and a minimum width of 30 m for linear elements such as shelterbelts and riparian corridors have been recommended (Freudenberger 1999; Freudenberger and Harvey 2003). Research has also shown that landscape context is important. The amount of habitat surrounding a revegetated patch is influential in determining the bird species richness of the patch as the surrounding habitat may provide additional habitat and facilitate movement through the matrix (Lindenmayer et al. 2010). Proximity of the patch to existing canopy was based on generic foraging and dispersal movement distances determined from a review of mammal and bird behaviour and landscape structural connectivity of south-eastern Australian forests and woodlands (Doerr et al. 2010). The review concluded forest and woodland species were unlikely to cross gaps more than 100 m wide and unlikely to disperse more than 1.1 km between patches. This limit to dispersal is similar to the figure of 1,000 m between patches specified by Freudenberger (1999). The distance of individual revegetation patches from woody canopy was calculated from a Euclidean distance calculation in ArcMap 10.1. Area–edge ratio for each patch was calculated from separate area and perimeter values.

Potential of revegetation to improve biodiversity

Revegetation sites were examined for their relationship to the predicted occupancy and metapopulation capacity values obtained from a Rapid Evaluation of Metapopulations (REMP) model of a woodland and dry forest specialist generic focal species (GFS; Foster et al. 2017b).

REMP is a process-based spatial modelling approach that synthesises metapopulation ecology and landscape ecology (Drielsma and Ferrier 2009) to integrate biological processes with landscape habitat patterns. REMP has been used previously to evaluate the effect of changed land use arising from an off-set programme on the predicted persistence of selected species of conservation concern in the far west of NSW (Drielsma et al. 2016). In our current study, the GFS represented species in the region susceptible to habitat fragmentation due to their ecological traits. These traits include poor dispersal ability, habitat specialisation and a requirement for large areas of habitat (Doerr et al. 2013). As a surrogate, the GFS was designed to also represent other species less susceptible to the effects of fragmentation. An evaluation of the GFS model determined the preferred model parameterisation (Foster et al. 2017a) and we use that model, hereafter referred to as GFS2, in this evaluation study.

The revegetation locations were also examined for their relationship to a state-wide analysis known as Native Vegetation Management Benefits Analysis (NVMBA) (Drielsma et al. 2013). The NVMBA represented estimates of how overall biodiversity across NSW could benefit from site-specific conservation action. The NVMBA mapping consisted of four benefits layers and the actions suited to these zones: (1) maintain current management within good condition vegetation (hereafter referred to as Maintain); (2) revegetate cleared areas (hereafter referred to as Revegetate); (3) improve vegetation condition of remnants (hereafter referred to as Improve), and (4) Landscape Value, relating to structural connectivity (hereafter referred to as LV). The first three layers use vegetation communities as a surrogate for biodiversity and relate actions to improvements in vegetation condition and extent. LV relates actions to improvements in broad-scale vegetation connectivity (Drielsma et al. 2013). The NVMBA broad-scale perspective was complemented by a regional connectivity analysis (Foster et al. 2016). Regional connectivity was derived from an adaptation of the LV analysis and was designed to capture regional-scale movement such as daily foraging in smaller habitat patches, within the broader-scale dispersal and

migration zones of LV. A feature of these multiple layers is their spatial overlap across the study region, implying a single revegetation site may contribute multiple and variable benefits related to species occurrence, vegetation condition or structural connectivity, depending on the theme of interest. Assessment themes are summarised in Table 1.

Theme values were standardised from 0–100 for ease of comparison. Analysis consisted of statistics generated from the Zonal Statistics as Table toolset (Spatial Analyst) of Arc Map 10.1 and graphical representations of the outputs. The Zonal Statistics toolset summarises the values of a raster (e.g. the LLS revegetation sites) within the zone of a second raster (e.g. a state-wide NVMBA layer). Graphs were produced in R (R Core Team 2016) and Excel.

The area of revegetation was compared with the assessment theme values divided into three ranges: low (<40), intermediate (40–80) and high (>80). The high ranges of the NVMBA and the regional connectivity layers indicated highly cleared, degraded and fragmented formations. Interventions in these areas will have highest benefit to biodiversity. Alternatively, the low range indicated vegetation formations which were least cleared, degraded or fragmented, thus interventions in these areas will have lesser benefit as existing conditions currently favour biodiversity. GFS2 occupancy and metapopulation capacity values <40 indicated a low probability of occupancy and low metapopulation capacity and values >80 indicated a high probability of occupancy and high metapopulation capacity. Our approach was to devise a 'rule of thumb' based on the premise that revegetation undertaken in regions of intermediate values of the landscape attributes would result in greater benefit to conservation (Tambosi et al. 2014). Species do not respond equally to revegetation (Lindenmayer et al. 2018) but as it was not possible to devise species-specific responses, our approach generalised the GFS2 response. In highly degraded landscapes, many species may already be lost and large amounts of restoration may be required for their recovery but success is uncertain. Where landscapes remain well connected or where species are abundant, restoration may not be required or may occur through

passive or autogenic processes. Targeting intermediate landscapes focuses on species which are susceptible to habitat loss and fragmentation but which remain sufficiently abundant to colonise the new habitat patches (see Tambosi et al. 2014). Thus, our criteria for the successful location of small revegetation patches was for the majority of hectares to occur within the intermediate range, with fewer hectares in the low and high ranges. Plots were constructed to (1) examine patch sizes across each range, and (2) examine the area of revegetation across each range.

Results

Patch design

The size of individual patches ranged from <1 ha to 35.6 ha (mean of 2.9 ha). The majority of sites, however, were <2 ha (154 sites, or 71.3%) with 100 sites <1 ha in size (46.3%) (Fig. 2). Mean patch size across the low, intermediate and high ranges of each assessment theme varied from 0–7.3 ha, with the larger patches falling within the high range for Revegetate and Improve themes and the low range of metapopulation capacity (Table 2).

Patch perimeter ranged from 85 m–10,747 m (mean 1,149 m) and width ranged from 6 m–732 m (mean 108 m). The minimum patch length per hectare was 68 m (area–edge ratio of 0.0146) and the maximum was 3,840 ha^{-1} (area–edge ratio of 0.00026; Fig. 3), with 183 sites (85%) below the area–edge ratio of 0.0029 of a circle (perimeter of a 1 ha circle = 345 m).

The proximity of sites to existing vegetation ranged from 0–807 m (mean 489 m). One hundred and eighty five sites (86%) were within 100 m of woodland canopy (mean 18 m), with the remaining 31 sites located more than 100 m from the presence of canopy (mean 232 m).

Improving biodiversity

The median values of the 216 revegetation sites were within the preferred intermediate range for GFS2 occupancy and the NVMBA layers Revegetate and Improve but were in the low value range for the remaining assessment themes (Fig. 4).

Most of the study region was categorised in the low range for all themes, except the NVMBA state-wide Improve and Revegetate layers which were mostly with the intermediate range. Clear patterns between the location of sites and the area revegetated were evident across the themes, with the higher proportions of sites and area revegetated located consistently in the most extensive range of each theme (Table 3). That is, the greatest proportion of sites and area revegetated occurred where GFS2 occupancy was predicted to be absent or low, where the metapopulation capacity of the landscape, regional connectivity and LV were low and where there was a low benefit from undertaking revegetation in the Maintain zone. However, the greatest proportion of sites and area revegetated were located in the intermediate range for the Revegetate and Improve themes. The least amount of revegetation and number of sites occurred in the high range of all themes (Table 3).

An example of the pattern in distribution of individual patch size is shown by the predicted occupancy of GFS2 (Fig. 5). Most sites (188 sites) were <5 ha in size and dispersed evenly across the low, intermediate and high ranges of predicted occupancy (Fig 5 left panel). The mean patch size of the low range was 3.0 ha (Table 2), but notably, four larger-sized patches (10–22 ha) were established in areas where no occupancy was predicted to occur. A second group of larger patches (10–36 ha) was located in the intermediate range of predicted occupancy, but mean size of all 88 revegetation patches in this zone was similarly 3.0 ha (Table 2). The total area of predicted occupancy across the intermediate range was low and coincided with a comparatively high amount of revegetation (Fig 4 right panel). The high occupancy range contained the least hectares of revegetation with a mean patch size of 1.9 ha.

Patches >10 ha were located mainly in the low and intermediate ranges for metapopulation capacity but were restricted to the low ranges for regional connectivity and the state-wide LV theme (Fig. 5 left panel). Patches >10 ha were situated in the intermediate and high ranges for the state-wide Revegetation and Improve themes. Smaller patches were located in the low range of all themes and dispersed within the intermediate range for the Maintain theme and high range for metapopulation capacity. Closer examination of the metapopulation capacity theme revealed most revegetation was located on the cusp of the low and intermediate value ranges.

Discussion

Published reporting on evaluation of local revegetation initiatives has occurred in other rural areas of Australia (e.g. site-based attributes of plantings in the South West Slopes region of New South Wales; Lindenmayer et al. 2013). In our study region, limited site-based evaluation of revegetation has been conducted by NRM agencies (Hawes 2016), and this study is the first landscape-scale evaluation into the effects of revegetation on biodiversity. The works were assessed for patch design features and their spatial location relative to modelled biodiversity management themes, where greater biodiversity benefit was assumed to arise from works implemented in the intermediate range of values of the assessment themes. Results revealed individual patches were predominately small, with high area–edge ratios located in the low range of values of the management themes. The establishment of a minimal number of larger-sized patches in the low range partially countered this negative result.

Small revegetation patches frequently dominate regional revegetation programmes (Smith 2008). An important consequence of smaller sized revegetation patches is the influence of edge effects on the provision of favourable resources for species. Species richness is also known to be greater in larger revegetated patches (Munro et al. 2011). Considerable research has focussed on the effects of habitat area, edges and their interactions (Ewers et al. 2007; Fletcher et al. 2007).

Edge effects describe ecological changes (such as energy flows, species movement, weed invasions, altered vegetation structure) that occur in the space between the ‘core’ of a habitat patch to the edge of a patch (Hobbs 1993; Ries et al. 2004). Small patches have a higher proportion of edge to ‘core’ habitat area (and therefore relatively less ‘core’) and are more susceptible to edge effects due to multiple edges in close proximity, resulting in an additive increase in the overall magnitude of edge-related changes. This underscores the need for larger-sized patches. The strength of the edge effects is dependent on the features of the surrounding landscape and the degree of contrast in vegetation structure between the patch and surrounding matrix (Franklin 1993; Ewers et al. 2007). Revegetation patches in agricultural landscapes provide an example of a strong structural contrast. Greater edge effects are experienced in long narrow strips and the effects may be more evident if the patch is open to stock grazing (Hobbs 1993). Grazing of revegetation and narrow strips have been associated with reduced likelihood of bird species (Lindenmayer et al. 2010) and the majority of works undertaken in the study region are required to exclude stock with fencing (L. Blair pers. comm.). Nevertheless, efforts to reduce further widespread establishment of small, high area–edge patches would provide for potentially higher quality habitat across the landscape.

The greatest benefit provided by revegetation was to improve vegetation condition, as seen by the dominance of sites in the preferred intermediate range of the Revegetate and Improve themes. The Improve theme targets existing remnants of regionally heavily cleared vegetation types with the Revegetate theme targeting action in cleared areas. The dominance of sites in these zones is perhaps unsurprising as, in this region, the intermediate range was the most extensive range for these themes. Conservation actions targeting existing remnants include infilling of patches, e.g. along riparian zones, and such activities were undertaken but the majority of patches were established in cleared paddocks or paddocks containing scattered trees.

None of the patches was beyond the distance considered the maximum for dispersal of woodland birds and mammals and most sites were within distance for daily forays. Therefore, from a modelling perspective, patches had the potential to act as stepping stones, facilitating species movement to new patches within the local landscape of the patch (Fahrig 2013). This is a desirable outcome; however, the majority of revegetation was established in regions where habitat connectivity, both regionally and at the broader state-wide level, was low. These placements may have been inevitable due to the large extent of poorly connected habitat across the study region with fewer options for placement in areas of intermediate connectivity. Low habitat connectivity at both regional scale and broader scale indicate severe habitat fragmentation. Most revegetation was also established where the capacity of the landscape to maintain GFS2 metapopulations was low—a corollary of low connectivity. While large amounts of revegetation were established in the intermediate range of predicted occupancy where it could expect to provide greater benefit, this benefit was overshadowed by the majority of revegetation being established where no occupancy was predicted to occur. Intuitively, these may be the preferred locations to establish revegetation in severely fragmented landscapes but small patches are predicted to have less effect, requiring either strategic placement of sites or sites to be more numerous or larger for maximum possible benefit beyond the local landscape of the patch (Munro et al. 2011; Haddad et al. 2017). The revegetation programmes incorporated in this evaluation were not limited to those with a primary focus on biodiversity and any evaluation on the success of individual projects would require the integration of many attributes, including those actions undertaken as part of the BNB project.

Limitations

One of the features of effective evaluation is confidence in the quality of the data. Several characteristics were noted which may affect the quality of the extracted data, however, they can be

summarised as inconsistencies in data entry practices and terminology between the two LLS that supplied the information. For example, a group of polygons with the same identifying number and attributed as ‘Establish vegetation’, may have also had additional activities such as ‘pasture cropping’ or ‘rotational grazing’. The lack of clarity in distinguishing which activity applied to which polygon required all polygons excluded from the analysis. Another inconsistency related to the amount of revegetation stated in the agreement with the landholder compared with the amount digitised in the spatial database. One LLS prioritised the agreements; the other LLS prioritised the spatial data. Our analysis prioritised the spatial data over the contractual data but either choice would have resulted in unavoidable uncertainty in the final data set.

Our evaluation made no quantitative conclusions regarding improvement in landscape habitat quality, species occupancy or species persistence resulting from the revegetation patches. The evaluation focussed on spatial location only—where in the landscape benefit might best arise. The reality of restoring habitat is that long time frames may be required to create habitat suitable for species. This may not always be the case (e.g. artificial nest hollows can immediately replace natural hollows) but real success may take decades (e.g. establishing mature trees) and still be of lesser quality than surrounding remnants (Maron et al. 2012; Lindenmayer et al. 2016). Another complication is the differing responses different species may exhibit to alternative temporal stages, with some species favouring early growth stages (less structurally complex) than later stages (Lindenmayer et al. 2016). Another complication is the differing responses of species to alternative temporal stages, with some species favouring early-growth (less structurally complex) stages than later stages (Lindenmayer et al. 2016). Although not used in this current evaluation, the habitat suitability estimate for revegetation in REMP reflects the potentially comparatively poorer quality of mature plantings (e.g. for GFS2, revegetation is 45% of the maximum value for each vegetation formation); however, it currently does not cater for species’ differing responses to alternative growth stages.

Evaluating the success of restoration planting can be problematic as, due to uncontrollable external factors, the progress of plantings may not always go according to plan. For example, the survival of plantings immediately post-establishment is uncertain, as many factors, including the weather, influence the outcome. Our evaluation assumes survival of the plantings. Our analysis was also a static evaluation, assuming security of plantings across time and tenure and constancy in the remaining landscape. However, our assumptions, both external to the methodology and those in-built, build a best-case scenario from which to judge the potential benefits of revegetation actions, and re-evaluations can be conducted in the future when improved information becomes available.

Finally, no indication was given of the total amount of revegetation that would be required across the region to maximise conservation benefit, information which could be useful to investors for identifying shortfalls. This could be achieved by extending the analysis to include an automated, iterative series of randomly located plantings using multiple runs of the model.

Conclusion

Evaluating revegetation activities is not often reported. This study conducted an ex post evaluation of revegetation activities undertaken by a regional NRM agency to judge the effects on improving biodiversity outcomes, while acknowledging that the suite of activities represented a variety of project objectives. We demonstrated the utility of incorporating a landscape and metapopulation approach to evaluation rather than site-based attributes of species diversity and abundance or vegetation structure, focussing instead on design features of the patches and the spatial relationship of the patches to biodiversity management themes. Spatial relationships were evaluated from a modelling perspective rather than empirical data. We found the activities to be dominated by numerous small patches, with the majority of revegetation area located within zones having a high priority for revegetating in cleared areas or improving existing remnants. However,

this positive assessment was overshadowed by the highly fragmented natured of the landscape, resulting in substantial amounts of revegetation established where we predicted it to have minimal potential for improving regional biodiversity. Increases in the number and size of patches, and greater cognisance of landscape context is required for greater potential gains in landscape connectivity and species occurrence.

This evaluation may assist the LLS with interpreting the direction of completed projects but it should not be viewed as an indication of failure of revegetation to remediate some of the regional effects of habitat loss and fragmentation on biodiversity. Evaluations should be an ongoing and adaptive process (Baker and Eckerberg 2016) during which time the effect of additional works can not only be incorporated, but new methods and criteria can be integrated into the assessment process. Additionally, multiple projects have multiple objectives and a patch may serve multiple benefits of which biodiversity benefits may be but one. NRM agencies can integrate this metapopulation style of analysis into an expanded assessment of project objectives to understand more fully the value of their investments.

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Table 1 Summary of themes used in the assessment of LLS's revegetation works

Theme	Description	Details	Taxa of interest	Reference
GFS2 predicted occupancy	Occupancy and distribution of populations for GFS2 were predicted via a metapopulation analysis estimating a landscape's metapopulation capacity	Output from Rapid Evaluation of Metapopulations analysis. Combinations of vegetation formations and land use used as a surrogate for vegetation condition. Expert-derived values for parameters habitat suitability, minimum viable habitat and dispersal and foraging distances. Analysis at 100-m cell resolution	Woodland and dry forest generic focal species (GFS2) composed of 10 species (bird, mammal and reptile) considered habitat specialists and sensitive to habitat fragmentation	Foster et al. 2017a (Chapter 4) and Foster et al. 2017b (Chapter 3)

GFS2 metapopulation capacity	The landscape's ability to support GFS2 metapopulation persistence into the future	as above	as above	Foster et al. 2017a (Chapter 4) and Foster et al. 2017b (Chapter 3)
Native Vegetation Management Benefits Analysis zones	Priority action zones for native vegetation management for species persistence across NSW.	Persistence modelled as the response to alternative management actions. Integrates vegetation composition, condition, spatial context and representation within a metapopulation analysis. Inputs were state-wide modelled vegetation classes and state-wide vegetation condition model.	see below	Drielsma et al. 2013
Maintain	Maintain current high vegetation condition of patches	Movement parameter values ranged from 2,000 m for cleared area to 5,000 m vegetation in high	Vegetation used a surrogate for biodiversity	Drielsma et al. 2013

		vegetation. Analysis at 250-m cell resolution		
Revegetate	Revegetate cleared areas would return highest benefit	as above	Vegetation used a surrogate for biodiversity	Drielsma et al. 2013
Improve	Improve current vegetation condition of existing patches (through infilling, buffering or revegetation)	as above	Vegetation used a surrogate for biodiversity	Drielsma et al. 2013
Landscape value	Link or retain current connectivity of remnants	Cross-scale connectivity based on habitat configuration and condition and species movement distances (31-500 km). Analysis at 400-m cell resolution	Wide ranging birds and mammals and rare longer distance movements undertaken by less mobile species	Drielsma et al. 2013

Regional connectivity	Landscape value enhanced with a finer-scale regional connectivity analysis to accommodate shorter daily movements. Referred to as enhanced regional connectivity in Chapter 2.	Identified potential dispersal links of 2.5 km between woodland habitat patches > 10 ha and < 100 m apart. Analysis at 25-m cell resolution	Woodland fauna	Foster et al. 2016 (Chapter 2)

Table 2 Number and mean size of patches (n = 216) across each value range for each assessment theme. Values of each theme are standardised from 0–100: low range = <40; intermediate range = 40–80; high range = >80. MPC = metapopulation; LV = Landscape Value

	Low			Intermediate			High		
	Mean patch size (ha)	Number of sites	Range (ha)	Mean patch size (ha)	Number of sites	Range (ha)	Mean patch size (ha)	Number of sites	Range (ha)
GFS2 occupancy	3.0	107	0.04–21.8	3.0	88	0.03–35.6	1.9	21	2.0–12.9
MPC	3.5	111	0.07–35.6	2.6	75	0.03–25.9	1.3	30	0.04–20.4
Maintain	3.0	178	0.04–35.6	2.3	38	0.03–16.1	0.0	0	0.00
Revegetate	1.9	30	0.04–17.4	2.9	181	0.03–35.6	7.3	5	0.4–16.7
Improve	1.0	5	0.8–13.5	2.9	186	0.04–35.6	3.5	25	0.03–16.7

LV	2.9	210	0.03–35.6	1.2	6	2.0–24.6	0.0	0	0.00
Regional connectivity	2.9	216	0.03–35.6	0.0	0	0.00	0.0	0	0.00

Table 3 Revegetation undertaken in low, intermediate and high ranges in each assessment theme (n = 216); MPC = metapopulation; LV = landscape value, BRG = Border Rivers – Gwydir catchment. Bold values indicate the highest value for each criterion per theme

	Low range						Intermediate range						High range					
Theme	Number of sites	Proportion of total sites	Hectares	Proportion of revegetation hectares	Extent in BGR region (ha)	Proportion of BRG region	Number of sites	Proportion of total sites	Hectares	Proportion of revegetation hectares	Extent in BGR region (ha)	Proportion of BRG region	Number of sites	Proportion of total sites	Hectares	Proportion of revegetation hectares	Extent in BGR region (ha)	Proportion of BRG region
GFS2 occupancy	107	**49.5**	313 3	**50.2**	2,823,342	**56.0**	88	40 7	234 3	37 5	765,891	15 2	21	9 7	77 5	12 4	1,451,606	28 8
MPC	111	**51.4**	371 7	**59.7**	3,150,675	**63.1**	75	34 7	212 4	34 1	1,424,100	28 5	30	13 9	38 3	6 2	415,275	8 3
Maintain	178	**82.4**	537 9	**86.0**	3,697,263	**72.8**	38	17 6	87 2	14 0	1,361,331	26 8	0	0 0	0 0	0 0	23,550	0 5
Revegetate	30	13 9	63 0	10 1	1,603,306	31 5	181	**83.8**	524 0	**83.8**	3,402,419	**66.9**	5	2 3	38 0	6 2	76,419	1 5
Improve	5	2 3	5 2	0 8	201,144	4 0	186	**86.1**	534 4	**85.5**	4,748,806	**93.4**	25	11 6	85 5	13 7	131,938	2 6
LV	210	**97.2**	617 1	**98.7**	4,441,481	**87.3**	6	2 8	8 0	1 3	638,938	12 6	0	0 0	0 0	0 0	4,694	0 1
Regional connectivity	216	**100.0**	624 7	**100.0**	4,166,048	**81.9**	0	0 0	0 0	0 0	903,769	17 8	0	0 0	0 0	0 0	15,038	0 3

Figure captions

Fig. 1 Conceptual framework to assess retrospectively the cumulative benefits to biodiversity of revegetation works undertaken within the Border Rivers – Gwydir catchment

Fig. 2 Number of revegetation sites plotted against combined area

Fig. 3 Patch length per hectare area plotted against patch area

Fig. 4 Box and whisker plots of standardised assessment theme values of the revegetation sites (n = 216 sites). Rectangles delineate the first and third quartiles, dark bars are the medians, the lower and upper ends of whiskers are the minima and maxima, and the dots are outliers. Dark grey panel indicates the preferred intermediate value range (40–80) of assessment themes; GFS2 = generic focal species; MPC = metapopulation capacity; LV = Landscape Value

Fig. 5 Revegetation works (ha) plotted against assessment themes; low range value = <40; intermediate range values = 40–80; high range value = >80 (left panel). Revegetation (ha) (left vertical axis) plotted against assessment themes (standardised values grouped in decile along horizontal axis) and regional extent of theme (right vertical axis). Deciles 0–4 = low values; deciles 5–8 = intermediate values; deciles 9–10 = high values; BNB = Brigalow–Nandewar Biolinks project and others initiatives; BRG = Border Rivers – Gwydir catchment. Numbers above bars = number of sites per decile (right panel)

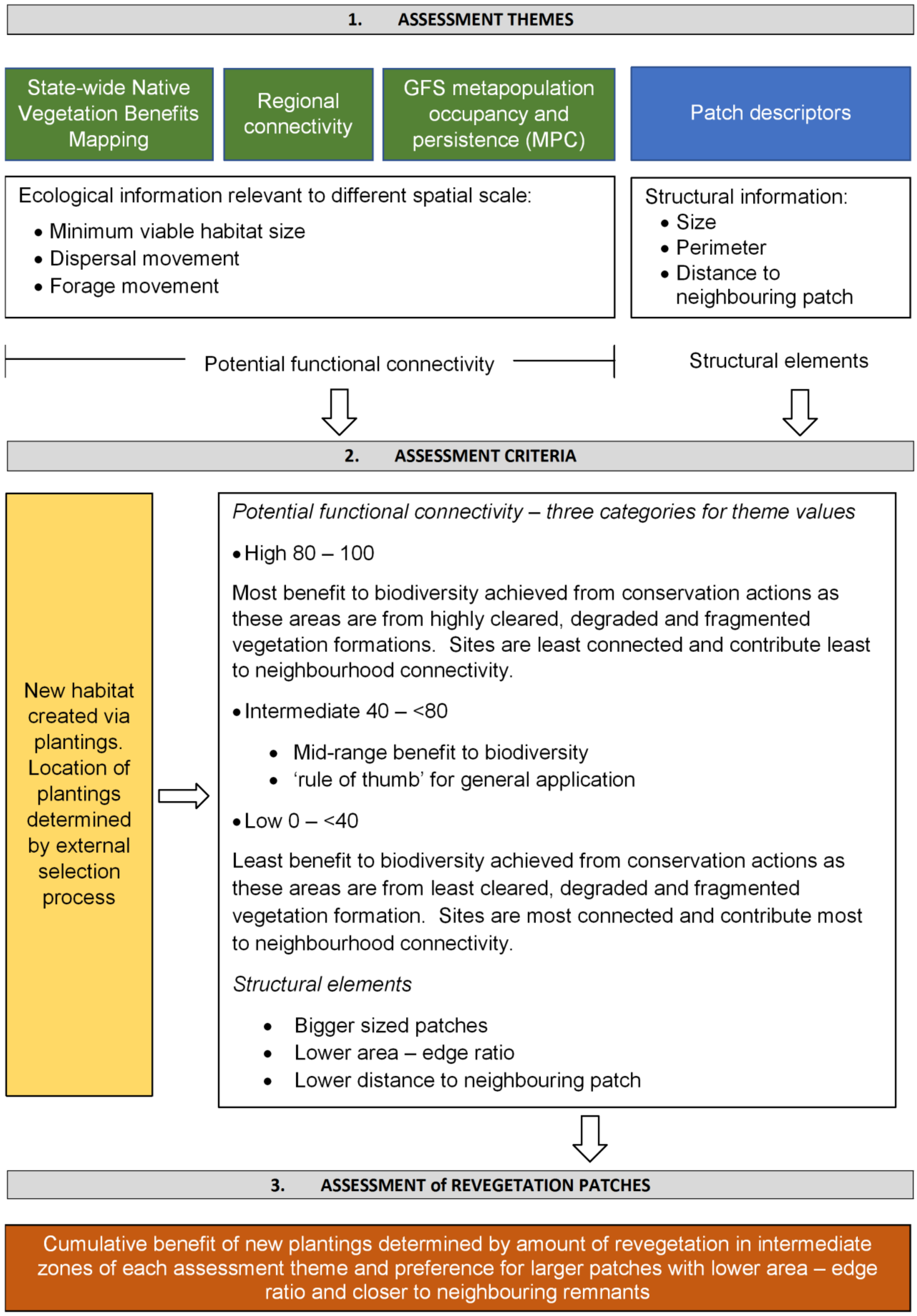

1. ASSESSMENT THEMES
State-wide Native Vegetation Benefits Mapping
Regional connectivity
GFS metapopulation occupancy and persistence (MPC)
Patch descriptors
Ecological information relevant to different spatial scale:
• Minimum viable habitat size
• Dispersal movement
• Forage movement
Structural information:
• Size
• Perimeter
• Distance to neighbouring patch
Potential functional connectivity
Structural elements
2. ASSESSMENT CRITERIA
New habitat created via plantings. Location of plantings determined by external selection process
Potential functional connectivity – three categories for theme values
• High 80 – 100
Most benefit to biodiversity achieved from conservation actions as these areas are from highly cleared, degraded and fragmented vegetation formations. Sites are least connected and contribute least to neighbourhood connectivity.
• Intermediate 40 – <80
• Mid-range benefit to biodiversity
• 'rule of thumb' for general application
• Low 0 – <40
Least benefit to biodiversity achieved from conservation actions as these areas are from least cleared, degraded and fragmented vegetation formation. Sites are most connected and contribute most to neighbourhood connectivity.
Structural elements
• Bigger sized patches
• Lower area – edge ratio
• Lower distance to neighbouring patch
3. ASSESSMENT of REVEGETATION PATCHES
Cumulative benefit of new plantings determined by amount of revegetation in intermediate zones of each assessment theme and preference for larger patches with lower area – edge ratio and closer to neighbouring remnants

Fig. 1

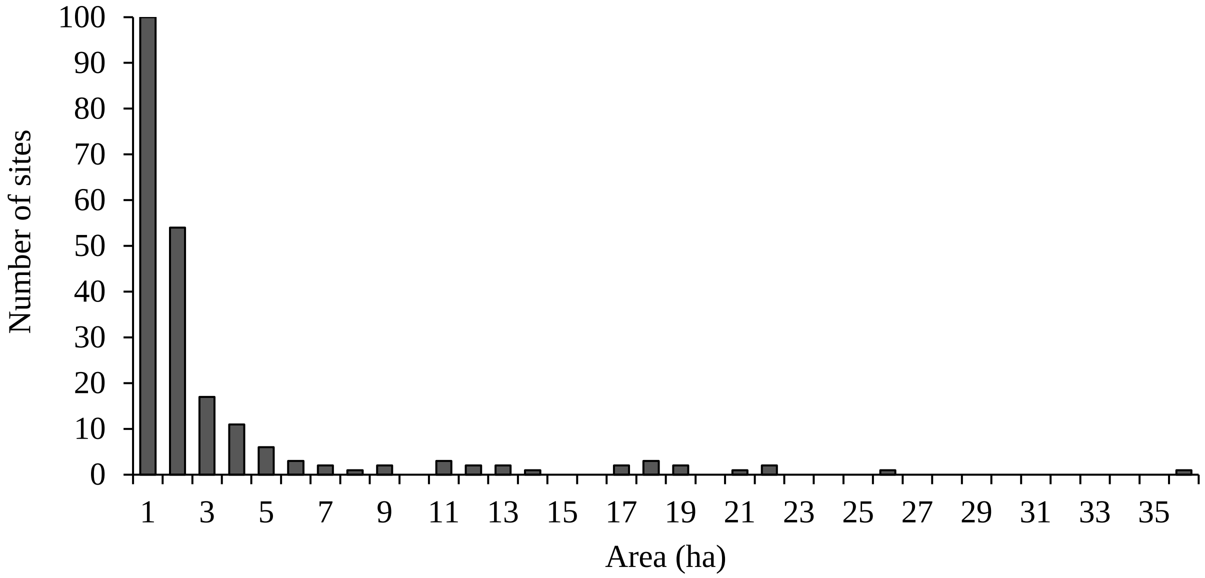
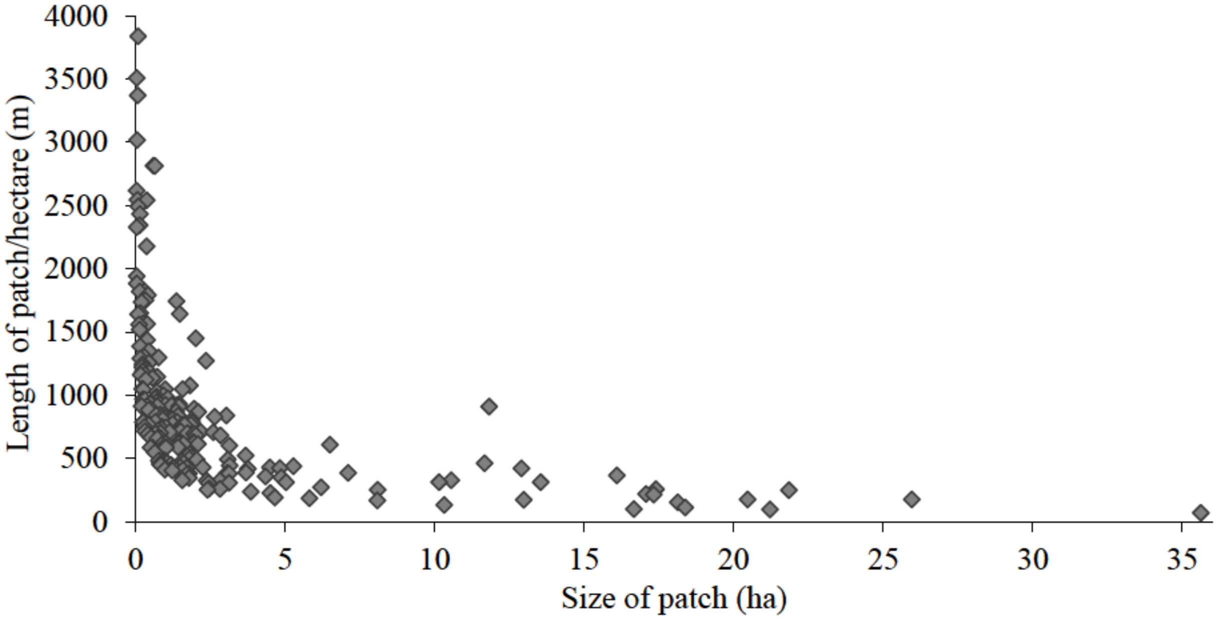
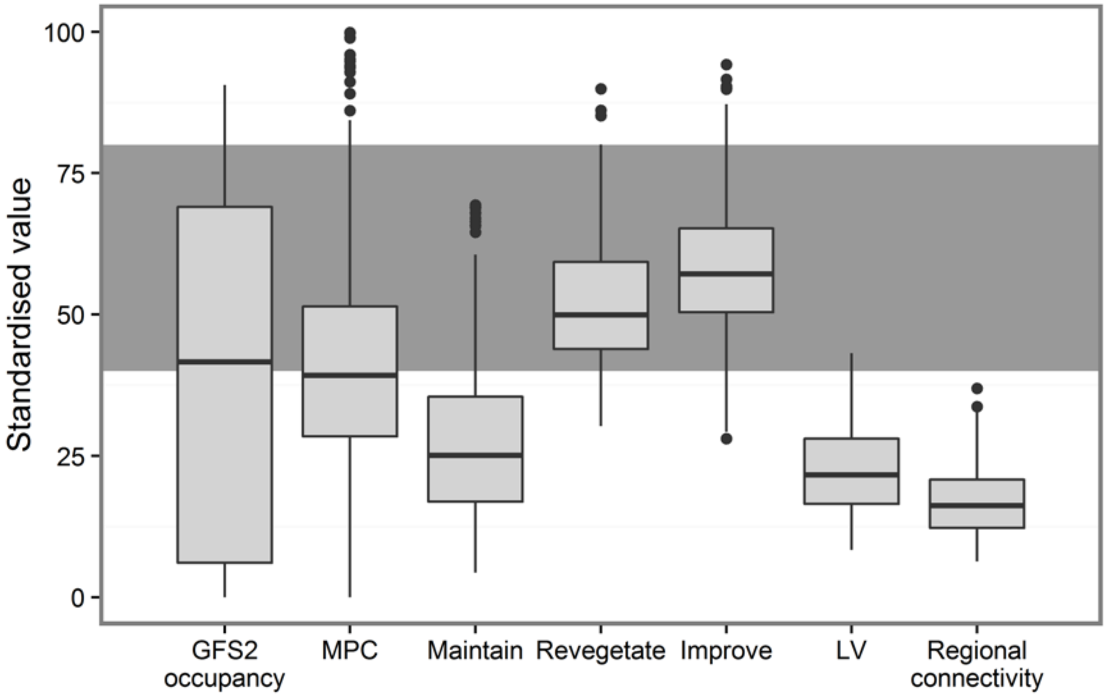

100
90
80
70
60
50
40
30
20
10
0
Number of sites
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35
Area (ha)

Fig. 2



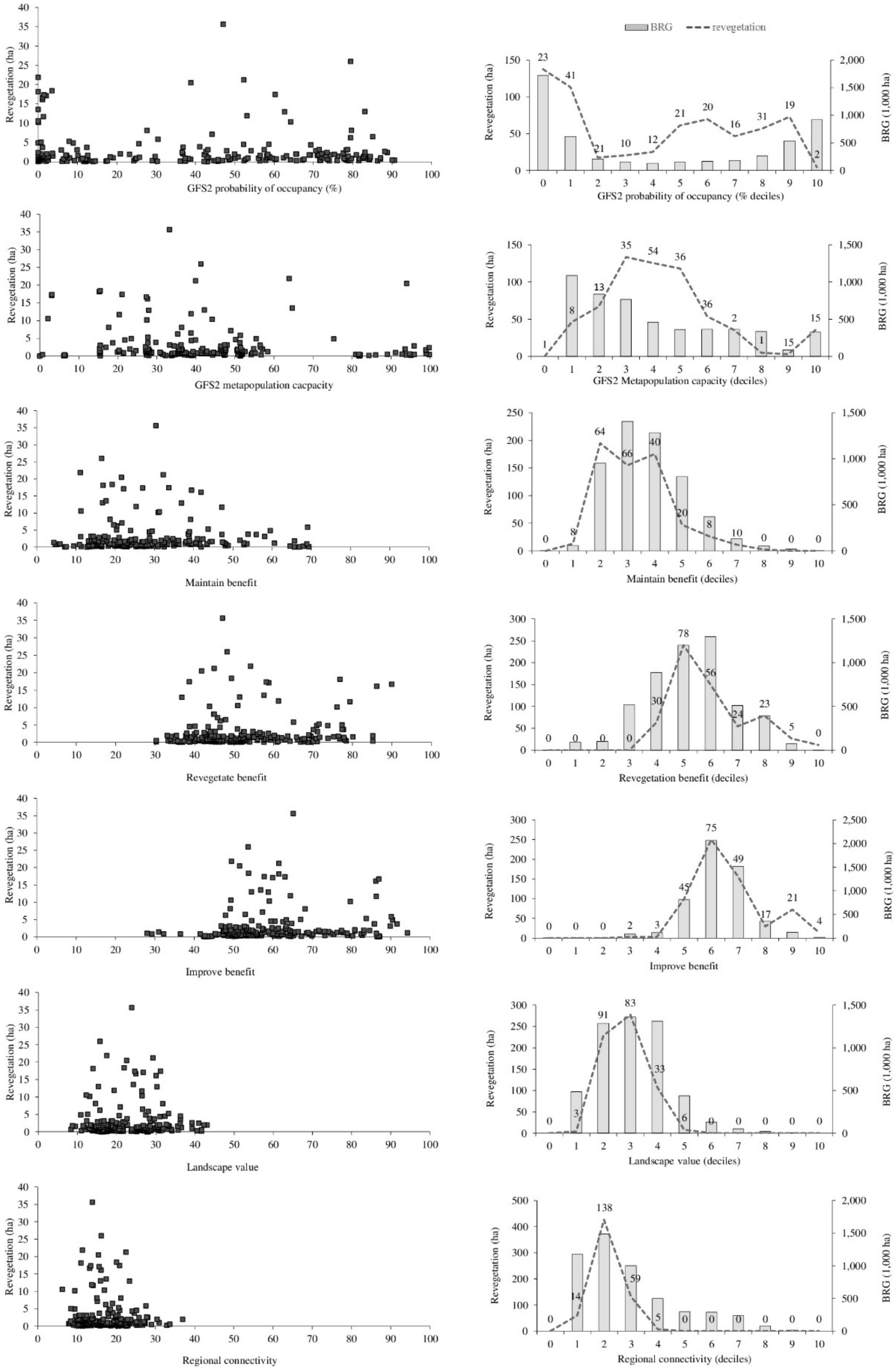
4000
3500
3000
2500
2000
1500
1000
500
0
Length of patch/hectare (m)
0
5
10
15
20
25
30
35
Size of patch (ha)

Fig. 3



Standardised value
100
75
50
25
0
GFS2 occupancy
MPC
Maintain
Revegetate
Improve
LV
Regional connectivity

Fig. 4



BRG
revegetation
Revegetation (ha)
BRG (1,000 ha)
GFS2 probability of occupancy (%)
GFS2 probability of occupancy (% deciles)
GFS2 metapopulation cacpacity
GFS2 Metapopulation capacity (deciles)
Maintain benefit
Maintain benefit (deciles)
Revegetate benefit
Revegetation benefit (deciles)
Improve benefit
Landscape value
Landscape value (deciles)
Regional connectivity
Regional connectivity (deciles)

Fig. 5

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Chapter 5 How effective are local revegetation programmes in conserving biodiversity in fragmented landscapes?

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We, the PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures, and diagrams are the candidate's original work.

Chapter 5 How effective are local revegetation programmes in conserving biodiversity in fragmented landscapes?

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Chapter 6

Conclusions and Synthesis

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1 Introduction

The aim of this research was to use metapopulation theory and landscape ecology to provide biologically relevant guidance on how to improve landscape connectivity in a fragmented agricultural landscape, through an on-ground revegetation programme. The aim of this chapter is to:

(1) summarise chapter by chapter the main findings of the thesis;

(2) present a synthesis of these findings;

(3) briefly discuss limitations of the research to identify areas of improvement;

(4) comment on the conceptual significance of the research;

(5) discuss the practical significance of the research, and

(6) make recommendations for future research.

2 Summary of findings

2.1 A cross-scale model of connectivity

The aim of Chapter 2 was to develop a spatially explicit methodology for identifying and improving connectivity and provide natural resource management agencies with the knowledge base for implementing revegetation actions for maximum biodiversity benefit. The study (Chapter 2) was an example of collaboration between ecologists, spatial researchers and on-ground practitioners, bridging knowledge gaps to better inform management options for improving connectivity. A methodology was developed and adopted as a fit-for-purpose means to meet the immediate needs of an agency engaged in connectivity restoration activities. The

hierarchical approach interpreted local improvements in connectivity within a metapopulation persistence context to achieve greatest biodiversity benefit for investment at local, regional and subcontinental scales in both the short and long term. The approach was not prescriptive and allowed for management actions to be tempered by local on-site considerations. As such, the products were considered the first step in a broader implementation process that includes engagement between NRM managers and landholders.

2.2 Dispersal linkages based on a GFS model

The aim of Chapter 3 was to apply metapopulation theory to a fragmentation-sensitive generic focal species (GFS) of specialist woodland and forest vertebrates and predict landscape capacity for persistence, the distribution of persistent GFS populations and their potential dispersal pathways to highlight connectivity gaps between populations. Chapter 3 revealed that the landscape had variable capacity to maintain surrogate populations across the study region. This resulted in a complex pattern of occupancy distribution and associated dispersal links. In areas beyond population boundaries, low-value dispersal links offered important opportunities for revegetation planning. In these instances, improving habitat could be achieved by revegetating to infill or enlarge existing patches or creating linear corridors between patches. The current landscape in our study region, however, presented few options for linking populations. In the east of the study region, revegetation action was not a priority as habitat connectivity and landscape capacity were sufficient to maintain a single population. In the central north–south subregion, regional inks were few in number and sparsely distributed but no populations were predicted to occur. In the west of the region, habitat clearance and modification has been extensive, resulting in a fragmented landscape with capacity to support a limited number of scattered populations and little opportunity to link populations. The only guidance for revegetation to improve connectivity came from broad-scale Landscape Value mapping.

2.3 A landscape's capacity to support wildlife

The aim of Chapter 4 was to gain insight into the relationship between two representations of habitat suitability—one indicated by past observations of species and the other being GFS predicted occupancy—in order to influence restoration actions. The two representations of habitat suitability were not closely aligned and although the analysis was not definitive due to demonstrated bias in the empirical data, the conclusion was that the representations provided differing perspectives of habitat use. The indications were that habitat suitable for supporting current occupancy and future long-term occupancy are distinct and a possible lag effect was occurring in the central subregion of the study region. Where such an extinction debt is potentially occurring, high impact remedial actions, such as revegetation to reconnect habitat, are required to arrest likely imminent extinctions.

2.4 Evaluating revegetation activities

The aim of Chapter 5 was to evaluate recently established revegetation in the study region in relation to two questions: did the design of the revegetated patches conform to aspects known to influence biodiversity response to revegetation, and was revegetation located where it had the potential to contribute greatest benefit to biodiversity? The revegetation activities were dominated by numerous small patches with high area–edge ratios, but with the majority of revegetation area located within high-priority zones for either revegetating cleared areas or for improving existing remnants. None of the patches was beyond the distance considered the maximum for dispersal of woodland species and most sites were within the distance of daily forays. Therefore, from a modelling perspective, patches had the potential to act as stepping stones to larger woodland habitat patches. This positive assessment, however, was overshadowed by the substantial amounts of revegetation established where it was predicted to have minimal potential for improving surrogate occupancy and, hence, regional biodiversity in the longer term. The revegetation was placed in highly fragmented sections of the landscape, corresponding to low

predicted occupancy and consequently, with a low potential for species to move into the new patches and increase regional occupancy. Increases in the number and size of patches and greater cognisance of landscape context is required for greater potential gains in landscape connectivity and species occurrence. The chapter provided a useful demonstration of a novel application of metapopulation concepts.

3 Research synthesis

The research can be viewed from two perspectives: the combined results as they relate to the study region, and as a generally applicable, multi-faceted approach to improve regional landscape connectivity and to identify locations for revegetation investment and monitoring.

The GFS metapopulation results for the study area revealed three distinct subregions—the eastern, central and western subregions—based on variable potential dispersal links and predicted populations. Consequently, there was a different emphasis across each subregion on the role of revegetation to improve connectivity or to link populations. In the eastern subregion, revegetation would have a minor role as populations are currently linked through contiguous habitat and underlying dispersal links. In the western subregion, however, linking disjunct populations will be difficult to achieve. This was due to the highly fragmented nature of the habitat and any populations predicted to occur are isolated from each other with little intervening habitat of sufficient quality or configuration to encourage dispersal. The landscape of the central subregion is highly cleared with relictual patches of habitat set amongst urban and intensive agricultural development. Here, an active extinction debt is likely occurring and revegetation to establish new plantings or expand relict patches is required urgently. Habitat connectivity is a strong driver of these results across all subregions. The clear distinctions in population and habitat distributions might suggest that in this study region, the metapopulation approach provided less practical outputs for planning purposes than the regional-scale, generic dispersal-based understanding of

structural connectivity and the broad-scale management zones presented in the second chapter. However, if viewed at a finer scale and used in conjunction, the metapopulation approach could supplement the first approach by identifying more nuanced, local priorities for action based on future species persistence. The question of whether these opportunities across the study region are being utilised by revegetation efforts undertaken by the LLS was partially answered. Much more additional work—either in the number of patches or larger patch size, and cognisant of landscape context—is required to make potential gains in landscape connectivity and species occurrence.

The conclusions arising from the combined results suggests that the threat of habitat fragmentation to biodiversity is currently more acute in the western and central subregions of the study region, where spatial solutions to restoring connectivity may be difficult due to the highly fragmented and relictual nature of remnant habitat, respectively. In these areas and without intervention, long-term biodiversity persistence will diminish over time due to poor current landscape capacity. Restoration plantings conducted to date will have limited effect in reducing this problem. This lack of impact of new plantings, however, is not limited to the central and western subregions, it is a region-wide issue. Considerable effort will be required on the part of implementing agencies to engage further with landholders to reduce the scale of the problem. Any planning of restoration actions needs to re-focus on increasing the total area of new planting and size of individual patches. The location of these plantings should concentrate on the regional-scale or broad-scale connectivity zones, the native vegetation management benefit zones, or gaps in the dispersal links between predicted populations. Sites which are located in more than one of these zones will accrue multiple benefits for connectivity and biodiversity benefit.

The combined elements of the research form a generic methodology, underpinned by metapopulation and landscape ecology principles, for improving regional connectivity through revegetation. The figure first presented in the Introduction (Fig. 1) can now be expanded to an

operational framework, outlining where to initiate regional programmes, and how to assess the impact of alternative revegetation schemes and monitor the progress of implementation (Fig. 2). The methods for deriving generic regional connectivity and benefits zones (demonstrated in Chapter 2), the REMP predicted occupancy model using a surrogate for biodiversity (Chapter 3) and the capacity of the current landscape to support future biodiversity (Chapter 4) could be applied by the NRM agency individually (as in Fig. 1) or in combination. Monitoring the implementation of programmes and assessing the biodiversity outcomes allows for an adaptive approach to continuing programmes, which may result in the evaluation of alternative revegetation scenarios. Monitoring may consist of the methods described in Chapter 5 or, after sufficient area of revegetation has accrued, of an evaluation through the REMP modelling system, seeking regional changes in REMP metrics as well as local spatial changes to occupancy in the vicinity of each newly planted or expanded patch.

4 Research limitations

Limitations and improvements to the study were identified in each chapter and are summarised here. The reduction of vegetation to a single structural class in the new local-scale and regional-scale connectivity analyses (Chapter 2) presented some limitations. Qualifying vegetation as a mosaic of woody/non-woody habitat ignored other structural vegetation types such as shrubland and grassland, which are an important but lesser areal component of the habitat mix in the study region. These are important for some taxa, such as ground-dwelling reptiles. Nevertheless, the binary definition of vegetation cover acknowledged the conservation significance of woodlands in southern and eastern Australia. The cost grid used in the calculation of the spatial links (Chapter 3) is an indication of landscape permeability and was derived from land-use information. Cost calculations could have been improved by the inclusion of influential factors, such as land tenure or abiotic environmental factors.

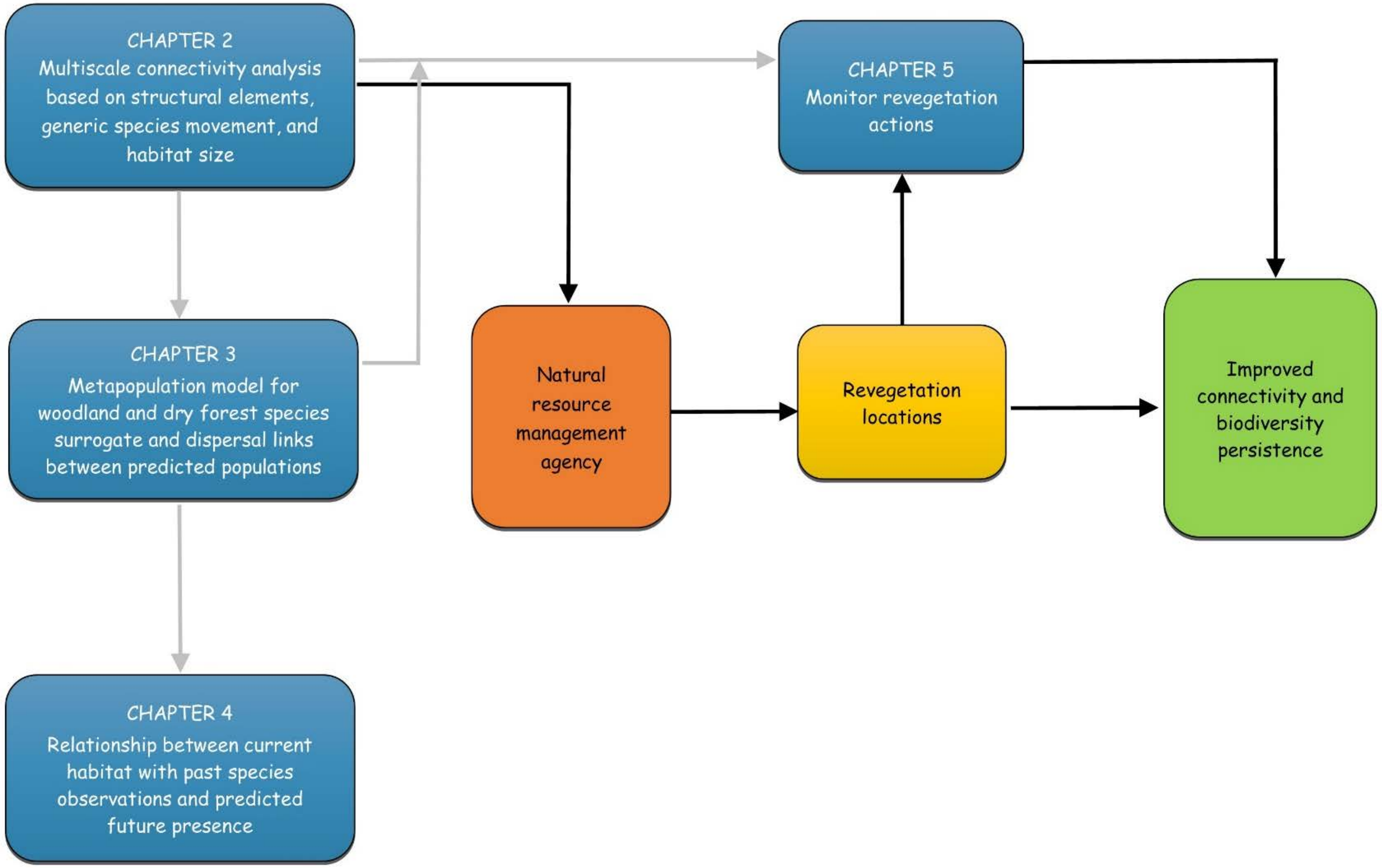
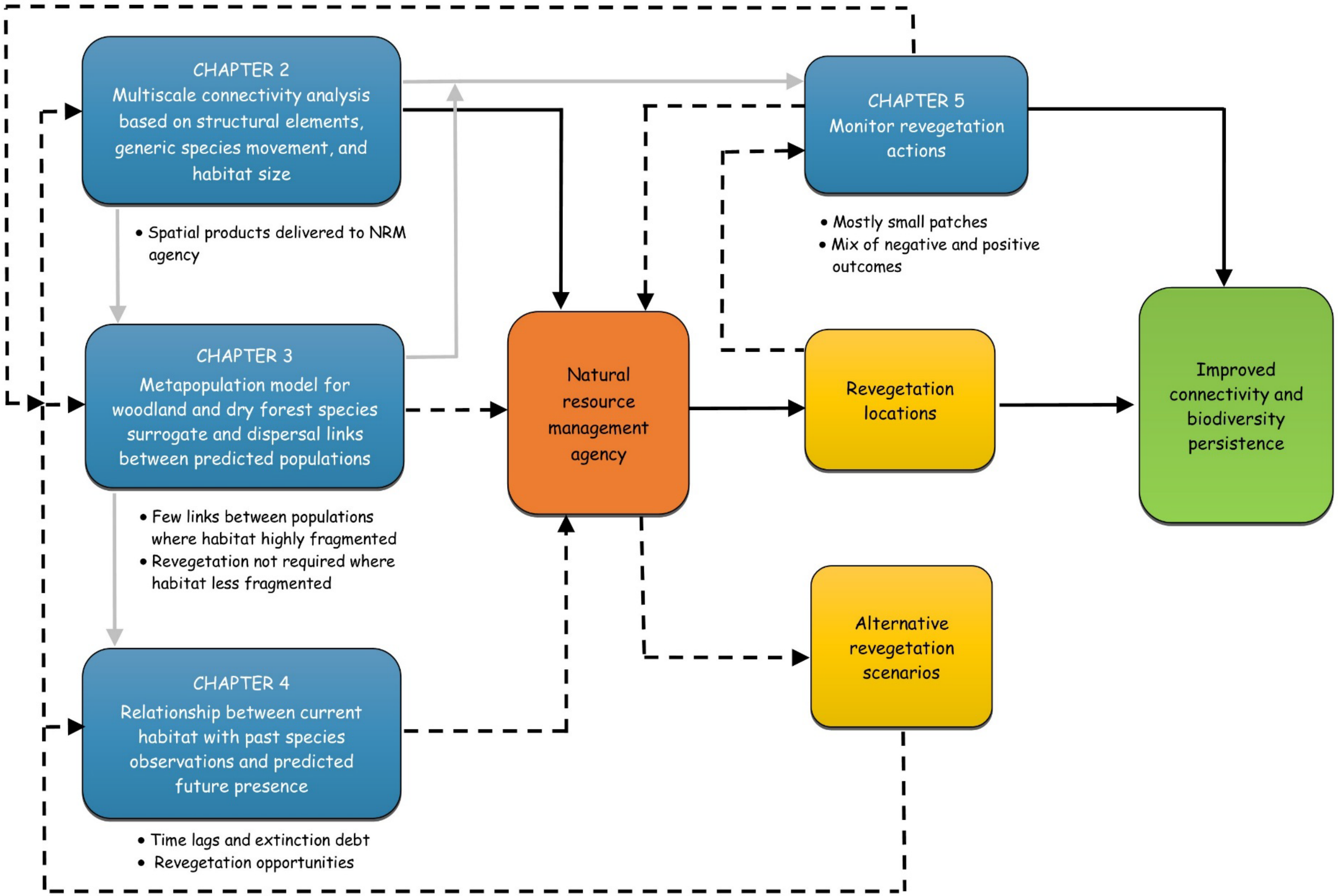


Fig. 1 Schematic representing chapters of the thesis and the connections to an NRM agency and biodiversity outcomes. Black lines represent pathways between chapters and outcome; grey lines represent links between chapters.



CHAPTER 2
Multiscale connectivity analysis based on structural elements, generic species movement, and habitat size
• Spatial products delivered to NRM agency
CHAPTER 3
Metapopulation model for woodland and dry forest species surrogate and dispersal links between predicted populations
• Few links between populations where habitat highly fragmented
• Revegetation not required where habitat less fragmented
CHAPTER 4
Relationship between current habitat with past species observations and predicted future presence
• Time lags and extinction debt
• Revegetation opportunities
Natural resource management agency
CHAPTER 5
Monitor revegetation actions
• Mostly small patches
• Mix of negative and positive outcomes
Revegetation locations
Alternative revegetation scenarios
Improved connectivity and biodiversity persistence

Fig. 2 Amended Fig. 1 from Chapter 1 Introduction, illustrating how the methods used in this thesis might be operationalised by a NRM agency. Research covered by the thesis is represented by solid black lines (pathways between chapters and outcome) and solid grey lines (links between chapters). The dashed black lines represent operational pathways (additional to the solid black lines) and bullet points summarise the main findings or outcomes for the study region.

Although the spatial data used in all the analyses were the best available at the time, spatial data inherently contain errors. These errors affect the determination of landscape pattern, including those arising from the digitising process (e.g. delineation of vegetation formations) and the qualification of attribute data (e.g. misclassification of land use). Land use is also a coarse surrogate for vegetation condition, a layer required by REMP. Consequently, discrepancies between coded land use and assumed condition at the site level could be encountered but were unavoidable. The GFS models may have benefited from an alternative vegetation condition layer derived from a separate GFS species distribution model that would subsequently be entered into REMP for calculation of predicted occupancy and landscape capacity.

The GFS was expected to replicate the constituent species but reducing 10 values to a single value for each parameter would have contributed to the poor alignment between observations and predicted occupancy (Chapter 4). The group is a mix of species that exhibit a variety of dispersal movements (e.g. combining a wide-ranging owl with a low-mobility reptile). Inevitably, the values for some species would have been under-valued or over-valued, blurring the congruence between species observations and predictions of occupancy. Woodlands are the dominant vegetation formation in the study region, and each species is considered sensitive to habitat fragmentation. However, the woodland and dry forest GFS used in our study was devised for a wooded landscape in another region. With further investigation, there could be additional data or alternative species to develop a local GFS that may better reflect local conditions. Constructing a GFS from species local to the study region may have also revealed additional or alternative fragmentation-sensitive species.

The observation data used in the assessment of current habitat for past species presence and future species occupancy (Chapter 4) were demonstrated to be biased and a larger, more systematic dataset could have been beneficial. However, complete and reliable field data on species is difficult and expensive to acquire. An alternative habitat surface for current species

presences could have been derived from a species distribution model. This could then be compared directly with the suitability surface from REMP to deduce the long-term potential for occupancy. A second alternative to improving the analysis could be for the habitat surface from the species distribution model to be entered into REMP as the required vegetation condition input, thereby combining both perspectives of habitat.

The assessment of revegetation actions (Chapter 5) was predicated on the assumption of the survival of all plantings and their immunity to stochastic events and unfavourable environmental conditions. Similarly, the effect of time on habitat quality and differing species responses to temporal stages of growth was not considered. Refinement of REMP parameters based on additional ecological data about species (where it exists) may be beneficial, but the lack of relevant data may be a limiting factor.

A final limitation of the general approach is the absence of the projected effects of climate change on species distribution and persistence. The contribution of remnant habitat patches to connectivity may change as species ranges shift in response to changing environmental conditions, with consequences for the future values of habitat networks and corridors (Gregory et al. 2014; Albert et al. 2017). Recent developments in REMP have addressed this shortcoming and provide an avenue for advancing the model outcomes.

5 Theoretical and conceptual significance of the research

Revegetation to improve connectivity across multiple scales and for the persistence of multiple species are recurring concepts in this thesis. There is precedence for integrating some of these concepts into conservation planning but not all concepts in the manner presented in this thesis. Examples include multiple species persistence for reserve selection (Nicholson et al. 2006), prioritising habitat patches for multi-scale movement connectivity (Rayfield et al. 2016), analysis of protected area connectivity relative to average dispersal distance of endemic bird species

(Maciejewski and Cumming 2016) and multiple species functional connectivity based on a cost surface derived from roadkill locations (Koen et al. 2014). Multiple species connectivity maps have been created from overlaying individual connectivity maps for individual focal species (Beier et al. 2009; Cushman and Landguth 2012) or multiple single species of interest (Gangadharan et al. 2017). The approach used in this thesis used one layer to determine connectivity for the species of interest (represented by the potential GFS dispersal links). Approaches specifically for planning revegetation include multi-criteria analysis to identify priorities based on broad ecological criteria, with or without incorporation of opportunity costs (Bryan and Crossman 2008; Zerger et al. 2011). Prioritising habitat patches for restoration has been based on vegetation type and distance to observations of birds of significance (Jellinek 2016). Crossman and Bryan (2009) defined natural capital hotspots to meet revegetation planning targets, where improvements in biodiversity, soil salinity and soil erosion could be achieved in a cost-effective manner. None of these four previous examples integrated metapopulation dynamics into their analyses. Metapopulation considerations and habitat context were accounted for, however, in a systematic prioritisation analysis to purchase land for restoration, with the aim of increasing habitat availability for persistence of two umbrella species (Crouizelles et al. 2015). Metapopulation dynamics, in the form of a population variability analysis, and landscape configuration were used to evaluate optimal alternative revegetation strategies (Westphal et al. 2003). The research presented here has an inherent flexibility to facilitate greater uptake by stakeholders and is not considered an optimisation method, and is not limited by requiring detailed ecological knowledge of the species of interest. Examples where methods for revegetation strategies have been implemented are few and have not included metapopulation dynamics (Westphal et al. 2007; Zerger et al. 2011). REMP has been applied to species management (Drielsma et al. 2016; Taylor et al. 2016) but this thesis represents the first applied use of REMP for informing on-ground revegetation efforts.

The broad findings of this research found that the study region fell, perchance, into three categories of habitat modification: relatively intact (eastern subregion), fragmented (western subregion) and relictual (central subregion). Revegetation options consequently varied for each region, with scale playing an important role. In the relatively intact landscapes of the east, where habitat is more broadly contiguous and biodiversity predicted to persist as a large single population, the requirement for revegetation effort is reduced but not negated. Fine-scale interrogation could reveal gaps and opportunities for engaging local landholders in NRM management options. Placement of revegetation effort in the gaps can also be guided by the management benefits and generic connectivity analyses which span regional and state-wide scales. Intersections of all zones provide for greater biodiversity benefit by supplementing and improving the networks for wider ranging movements, such as migration, shorter distances for forays, and local movement between populations. In the relictual habitat of the central subregion, revegetation efforts (such as improving the patch quality or matrix permeability) should necessarily concentrate on those isolated patches which might still contain species facing extinction. Efforts by NRM agencies in such subregions should therefore be more tightly targeted. Fragmented landscapes such as in the western subregion illustrate part of the continuum of modified landscapes and is where gaps in the pattern of potential dispersal links between discrete populations, or weaker links between populations, should direct effort. The role of scale and the multiple connectivity and benefits analyses play a similar role in this subregion as they do in the better connected, variegated habitat in the eastern subregion. Revegetation efforts by NRM agencies should be guided by a combination of local and broad-scale priorities. The concepts of landscape modification described at the level of the study region can be extrapolated to the global environment, where intensification of land use has wrought habitat change ranging from relatively unmodified to total removal of natural systems. The multiple-scale and multiple-species emphasis for connectivity and restoration have relevance in similar contexts worldwide.

Revegetation efforts undertaken in the study region showed a bias towards small patches, mostly located in regions where their effect on biodiversity was predicted to be limited. The motivations of landholders on private lands to become involved in revegetation efforts is a feature of restoration which can be overlooked but which is part of the complexities of the research–practice nexus (Wyborn et al. 2012). Research has shown that landholder participation in conservation measures can be driven by personal, social, cultural and economic factors, and failure to take up practices is often due to a lack of perceived economic benefit from the action, such as long-term funding and opportunity costs (Pannell et al. 2006, Sherren et al. 2010; Iftekhar et al. 2016; Pannell 2016). These concerns are not unique to Australia and are recognised in other international restoration projects (Franklin et al. 2014). Landholders are more likely to take up activities if they have previous experience of them (Jellinek et al. 2013) but continuing dialogue between all stakeholders—scientists, practitioners and landholders—and building capacity of local communities to undertake activities is recommended, both nationally and internationally, for successful ecological restoration (Burbidge et al. 2011; Newton et al. 2012; Wyborn et al. 2012). This research is an exemplar of science informing investment, adding to similar literature (Podolak et al. 2017). It is also an example of incorporating knowledge into institutional operations, allowing knowledge to feed back into monitoring and project evaluations, criteria which have been identified for successful incorporation of science into management (Burbidge et al. 2011).

6 Practical significance of the research

The analyses focus attention on candidate areas for investment and on-ground works, and the outputs require consultation with landholders to determine the actual areas where actions are to be undertaken at the property level. While this research identified areas that were of higher biodiversity importance, it did not prioritise one such area over another. In productive landscapes

where multiple interests and actors are present, sustainable planning and long-term maintenance of biodiversity can be achieved if there is are choices between alternative ecological design options to balance ecological social and economic requirements (Opdam et al. 2006). The methods used in this research identified broad connectivity and benefit ‘zones’, rather than highlighting specific patches, allowing institutions to target specific regions within their jurisdiction, followed by direct negotiation at the property level. For instance, flexibility in placement of new plantings or patch expansions may be required where habitat patches or gaps are evident in the field that are not evident in the remote sensing, or where negotiations are required to accommodate the specific social or economic interests of the landholder.

The practical significance of the research is further demonstrated by the uptake of the multi-scale connectivity analysis by the LLS as one of the assessment criteria for investment applications from landholders, as a starting point for on-site negotiations and for targeting incentive programmes. Further practical relevance of the research as an operational framework has been discussed in Section 6.3. Recommendations for implementation arising from the research are:

(1) the LLS take up the framework, or parts of the framework, e.g. monitoring component (Fig. 2);

(2) direct the planting of new patches or enlarging existing patches to where they can best improve predicted occupancy or connectivity in zones outlined in the spatial outputs, and

(3) larger sized patches of new plantings should be encouraged.

7 Future research

Several recommendations for future research can be made:

(1) In recognition of the coarse scale and nature of the land-use layer as a surrogate for vegetation condition, replace land use with a habitat suitability layer derived from a GFS species distribution model and examine the effects on predicted occupancy.

(2) Conduct a similar connectivity analysis in another agricultural region where land-use change has stabilised some decades ago and investigate the congruence of the GFS predicted occupancy model with observations. This would test the hypothesis in Chapter 4 that the extinction debt would have had more time to take effect, reducing its confounding effect on the congruence between observations and predicted occupancy, and therefore allowing greater certainty about the capacity of the landscape to support future populations.

(3) Collaborate with the LLS on the uptake of the framework, either wholly or in part, and investigate how the framework might be integrated into existing LLS schemes for prioritising on-ground restoration works. Investigate potential motivations and impediments to participation in revegetation programmes, and how any social goals or priorities that may exist in the community might be further integrated into the framework or the modelling system.

(4) Recent advances in REMP (since submission of this thesis) have incorporated the effect of climate change on biodiversity persistence and the role for revegetation. These advances should be used to improve connectivity and metapopulation persistence analyses in the study region for the benefit of investors.

(5) Investigate methods to address how much revegetation is required in the study region to achieve adequate benefit to biodiversity. Such methods might include an automated, iterative series of randomly located plantings in multiple runs of the model.

(6) Expand the parameter settings for revegetation that exist currently within REMP to integrate time horizons—that is, the temporal responses of plantings—in occupancy and metapopulation analyses. This would require robust new estimates for growth stages of restoration prior to maturity (which is the current setting) for each vegetation formation; however,

this information may not be readily available. This analytical refinement would also require a decision about whether the GFS exhibits similar occupancy in young and mature restoration of each vegetation formation, given that constituent species of the GFS may exhibit various levels of occupancy in different-aged restoration of each formation. A series of models could be run, using time since planting and the new parameterisation, to track the potential contribution of plantings to biodiversity.

8 Final thoughts

The impact of habitat loss, fragmentation and degradation of habitat remnants on the occurrence and persistence of biodiversity is a global concern. Improving habitat connectivity to help restore functioning landscapes is an urgent management issue. Successful restoration of landscape connectivity will only occur with the collaboration of all stakeholders—including landholders, the community, funding bodies and NRM practitioners—and management decisions require solid ecological foundations. The analytical approaches presented in this thesis can be adopted by NRM agencies to guide the placement of revegetation and for adaptively managing programmes. The research has demonstrated that considerable additional revegetation effort in the study area is required to rescue isolated habitat or populations. Continuing the collaboration between researchers and practitioners is strongly recommended as part of the solution to maintaining biodiversity.

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Appendix 1

Planning for metapopulation persistence using a multiple-component, cross-scale model of connectivity. Biological Conservation 195:177-186

Figure A.1: The methodological approach undertaken to integrate broad-scale NVMBA with fine-scale connectivity analysis within the Border Rivers – Gwydir catchment. Further detail on components can be found in Tables A.1 and A.2.

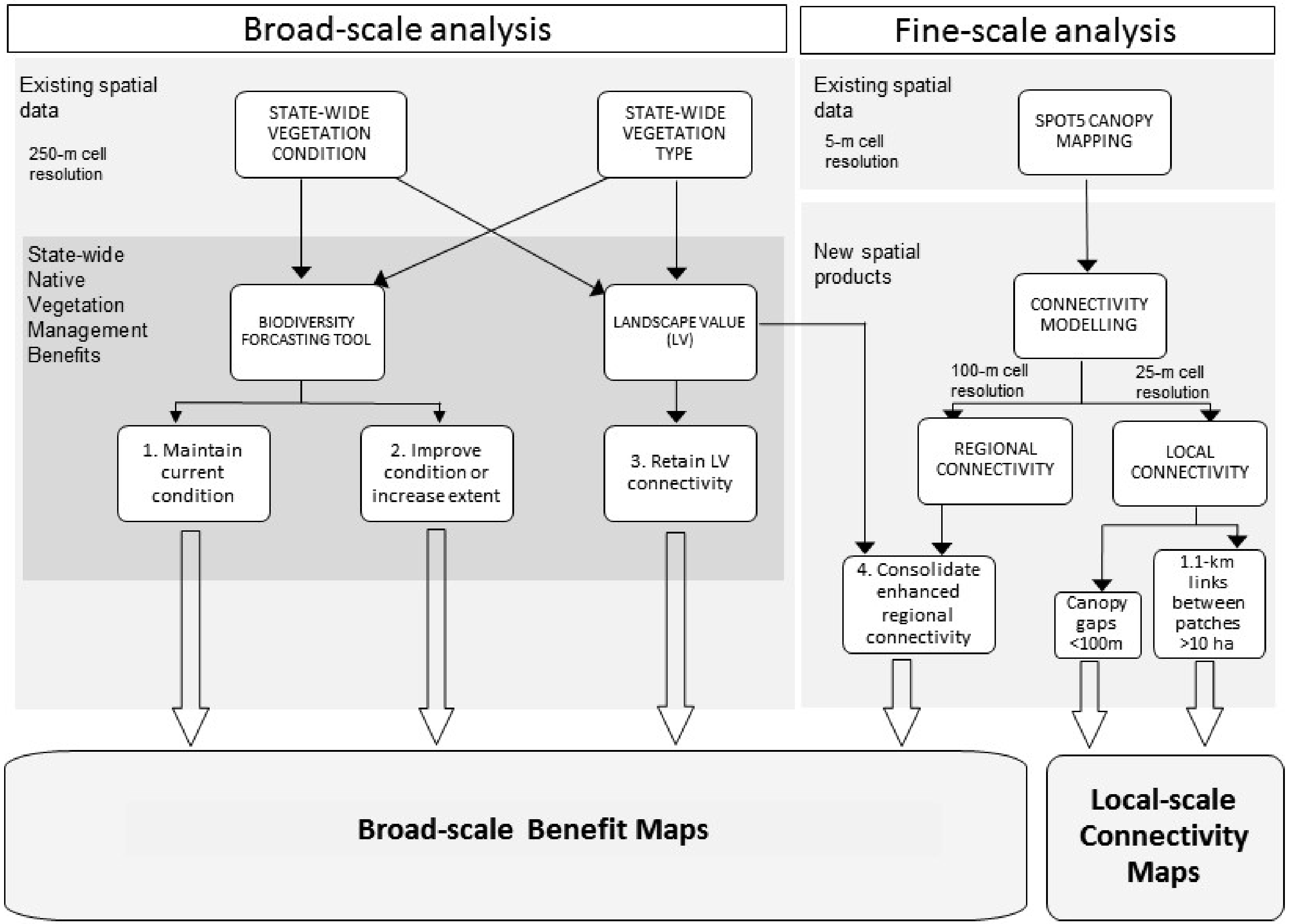


Table A.1: Process for determining broad-scale NVMBA outputs and the relationship to regional-scale and local-scale analyses.

Analysis/Data	Process	Scale	Process	Description	Technique	Input layers	Main Parameters			Outputs	Comments	End Product Map
							Movement Distance (km)	Cell resolution (m)	Link Length (km)			
Existing	Native Vegetation Management Benefits	State	Biodiversity Forecasting Tool (Drielsma et al., 2014)	Predicted persistence of biodiversity	1. Neighbourhood Habitat Analysis (NHA)(using Cost Benefit Approach (least-cost paths)) 2. Marginal Biodiversity Index	1. Generalised dissimilarity model (GDM) of vegetation class (benefit grid) 2. Modelled current vegetation condition (cost grid)	Values range from 2 km in cleared cells to 5 km in cells with maximum condition	250	NA	Benefits layers (individual) 1. Managing remaining examples of highly cleared vegetation classes (Keith, 2004) to retain current good condition and context. 2. Improving or increasing the area of highly cleared vegetation classes (Keith, 2004).	Vegetation used as a surrogate for all biodiversity	BFT and LV outputs combined for subcatchment scale benefit map
			Landscape Value (LV) (Drielsma et al., 2013)	Connectivity analysis	Habitat links Analysis (Spatial Links Tool using Cost Benefit Approach (least-cost paths))	Vegetation condition modelled for three broad vegetation structural classes - derived from SPOT-5 foliage projective cover	31.25 62.5 125 250 500	250 500 1000 2000 4000	25 50 100 200 400	Benefits layers (individual) 3. Consolidation of existing vegetation in good condition	Variety of cell resolutions used to reflect different scales of movement process e.g. daily	

						(closed forest, open forest and woodland) - to produce benefit and cost grids					foraging, dispersal and migration	
					Neighbourhood Habitat Analysis (NHA) (using Cost Benefit Approach (least-cost paths))	As above	4 – 10 times grid cell resolution.	As above	NA			

Cost grid values represent the cost (or effective)-distance for a species to traverse the width of a cell (Drielsma et al., 2007b). Benefit grid values represent the expected level of benefit an organism receives from resources at a cell (food, shelter, colonisation sites); referred to as habitat suitability (Drielsma et al., 2007a).

Table A.2: Process for determining local-scale (component 1) and enhanced regional-scale (component 4) connectivity analysis.

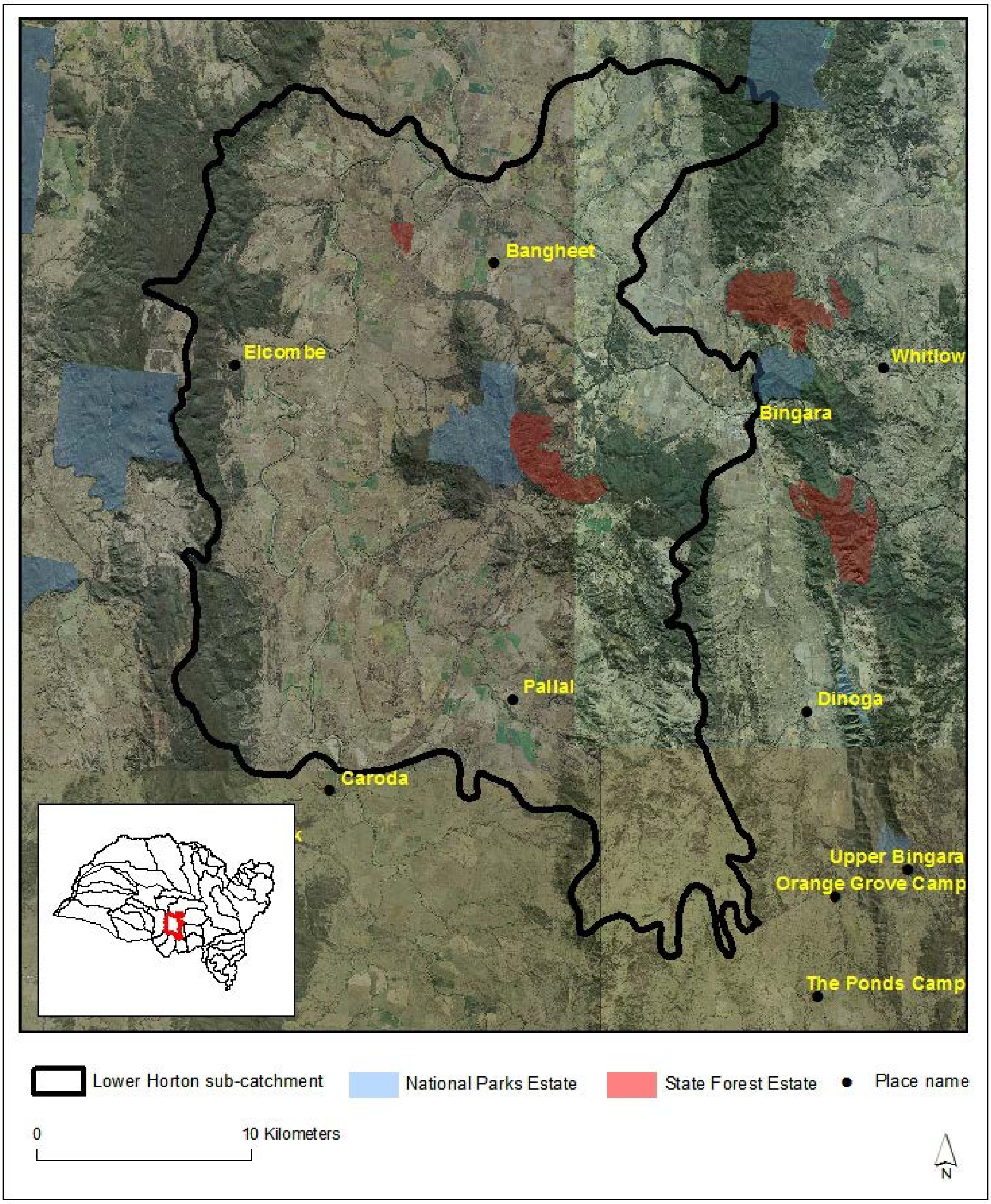
Analysis/Data	Process	Description	Scale	Technique	Input layers	Main Parameters			Outputs	Comments	End Product Map
						Distance measure (m)	Cell resolution (m)	Link length (maximum gap crossed) (m)			
New	Fine-scale Connectivity Modelling	Connectivity analysis based on state-wide parameters scaled down to suit reduced resolution	Regional (BR-G catchment)	Habitat links Analysis (Spatial Links Tool using Cost Benefit Approach (least-cost paths) (Drielsma et al., 2007b)	Canopy mapping (continuous woody/non-woody cover data to derive benefit and cost grids	2500	100	2500	Grid identifying high value links between suitable habitat patches representing the most ecologically efficient paths for moment through the landscape.	Regional connectivity layer. Supplements state-wide LV	Regional connectivity output combined with State LV to produce enhanced regional connectivity layer for subcatchment-scale Benefit map (Benefit 4).
		Connectivity analysis based on requirements of woodland birds and small mammals*	Local, across Landscape Regeneration project area	1. Habitat links Analysis (Spatial Links Tool using Cost Benefit Approach (least-cost paths)) (Drielsma et al., 2007b)	Benefit and cost grids derived from canopy mapping (binary data)	N/A	25	100	Grid identifying high value links between suitable habitat patches representing the most ecologically efficient paths for moment through the landscape.	Maps the extent of canopy (including stepping stones) with gaps <100 m (cleared: <= 100 m gaps = lower cost; > 100 m gaps = higher cost) Gaps identified by	Layer for local-scale map

										stipulating max distance an organism will travel through the landscape, given the cost value (expert derived)	
				2. Neighbourhood Habitat Analysis (NHA) (using Cost Benefit Approach (least-cost paths)) (Drielsma et al., 2007a)	Benefit and cost grids derived from canopy mapping (continuous data)	1000	100	NA	Habitat context	Identify connected habitat patches >10 ha	Binary habitat patches
				3. Least-cost paths analysis	Benefit grid derived from canopy mapping (continuous) and which was used mask binary habitat patches (from Step 2) Cost grid derived from continuous canopy mapping &	N/A	25	1100	Grid identifying high value links between suitable habitat patches representing the most ecologically efficient paths for moment through the landscape.		Layer for local- scale map

					100 m gaps (from Step 1)						

Cost grid values represent the cost (or effective)-distance for a species to traverse the width of a cell (Drielsma et al., 2007b). Benefit grid values represent the expected level of benefit an organism receives from resources at a cell (food, shelter, colonisation sites); referred to as habitat suitability (Drielsma et al., 2007a). * Movement parameters, link length and minimum habitat patch size for local-scale analysis taken from Doerr et al. (2010).

Figure A.2: Lower Horton subcatchment image showing state-owned reserves and forests (source: NSW Office of Environment and Heritage).



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Appendix 2

Integrating a generic focal species, metapopulation capacity, and connectivity to identify opportunities to link fragmented habitat. Landscape Ecology 32:1837-1847

Appendix S1. Study region

The natural vegetation of the Border Rivers – Gwydir catchment study region grades from humid high-altitude tableland forest in the east on top of the Great Dividing Range, through open-forest and woodland on the North-West Slopes of NSW in the central catchment, to low-elevation semi-arid open woodland, tall shrubland and grassy plains in the west. The regional economy is based around agriculture (grazing, dryland and irrigated cropping) and rural and regional services. The vegetation has been extensively cleared and modified. Since European arrival some 71% of the region's native vegetation has been transformed or altered through land use and management (DECC 2010), resulting in fragmented and variegated landscapes. The Brigalow–Nandewar Biolinks Project (BNB project) (http://www.agbiolinks.com.au) is being undertaken by the Northern Tablelands and North West Local Land Services (LLSs) to improve connectivity for biodiversity. The project was instigated in 2012 with AU$5 million of Australian Government funds to invest with landholders and the project's targets include revegetating 1,550 ha of cleared farmland.

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Appendix S2.

Predicting occupancy using REMP

REMP employed a species-focused approach in assessing landscape fragmentation by integrating biological processes with landscape habitat patterns. The integration of process and pattern has been recognised by other authors (Turner 1989; Ferrier and Drielsma 2010). In this study, the generic focal species took the role of the 'species'. With information on habitat preferences and movement behaviour, REMP used a Cost–Benefit Approach (CBA) (Drielsma et al 2007), utilising least-cost paths on grid surfaces that respectively represented the benefits afforded by access to habitat and the cost of accessing habitat, to produce a final grid which represented the connectivity of each cell to its neighbour. A benefit of using grid surfaces is the ability to easily accommodate the continuum of habitat variegation across the landscape and to account for changes in habitat permeability for organism movement (Fischer and Lindenmayer 2006; Drielsma et al. 2007; Drielsma and Ferrier 2009). This is a departure from patch-based metapopulation approaches, which view the landscape as a matrix of habitat and non-habitat, ignoring the significant contribution the matrix can make to species dispersal (Ricketts 2001; Fisher and Lindenmayer 2006; Eycott et al. 2010).

Modelling predicted occupancy used an approach modified from Hanski (1999) where the concept of a patch was replaced with the cell, and colonisation and local extinction were calculated using the CBA-derived connectivity values (Drielsma and Ferrier 2009). The final output was a probability surface where each cell had a value corresponding to the probability of the generic focal species occupying that location. The probability was based on the GFS's ecological characteristics for minimum viable habitat and movement distances and on habitat features such has shape, condition and context. The ability of the species to persist in the landscape (in response to habitat properties only) was calculated via metapopulation capacity

(MPC), a measure of the ability of the fragmented landscape to sustain a metapopulation. A species is predicted to persist in the landscape if the MPC value is greater than an extinction threshold value. A value below threshold indicates the species is at risk of extinction (Drielsma and Ferrier 2009). MCP can be used to rank different landscapes (Hanski and Ovaskainen 2000).

Permeability of the landscape (representing the energy cost to the organism of traversing the landscape) varies according to landscape pattern. Permeability is the inverse of cost: more permeable landscapes are less constraining to movement and therefore incur a lower movement cost to the organism. Permeability values ranged from 0 (providing the most inhibiting habitat and where the species will be less likely to disperse through the habitat) to 1 (least inhibiting habitat and where the organism can potentially move its maximum dispersal distance).

Dispersal links using Spatial Links Tool (SLT)

Colonisation potential calculated from (Hanski 1999):

$$P = H_i H_j W_{ij} \qquad \text{(eq 1)}$$

where H_i and H_j represent the habitat suitability value at the source i and destination j of each least-cost path. The dispersal kernel, W_{ij}, defined the permeability of the link and was calculated using the sigmoidal decay function:

$$w_{ij} = \frac{e^{-i(d_{ij}-{}^{1}/_{\alpha})}}{1+e^{-i(d_{ij}-{}^{1}/_{\alpha})}} \qquad \text{(eq 2)}$$

where d_{ij} represents the effective distance of traversing the path, calculated as the sum of individual cell cost values for all cells in the path, and *i* regulates the slope and width of the decay zone. ${}^{1}/_{\alpha}$ represents the average dispersal distance of the fauna concerned. Threshold values within the SLT set the environment for the identification of link connectivity values between site pairs.

Required parameter specification to run SLT included an estimate of the maximum dispersal distance (set at the REMP parameter of 3,300 m) and a maximum link search distance set at 6,600 m, the distance at which the tool would cease to search for connected pairs. A slope parameter of 0.0015 was set for the dispersal kernel. Analysis was conducted at 400-m cell resolution to accommodate broad-scale movements.

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Appendix S3. Datasets and GIS layer compilation

1) Vegetation extent

Vegetation data was a modelled probability surface derived from a generalised dissimilarity model (GDM) (see Ferrier et al. 2007 in Drielsma et al. 2013). Site vegetation data and spatial environmental predictors were analysed by the GDM to produce 125 state-wide probability surfaces, each representing a Keith (2004) vegetation class. Classes are defined by floristic similarities, and are numerous for NSW. For the purpose of the study, classes were grouped according to their vegetation formation, the highest level of the classification hierarchy. Twelve formations are defined for the BRG region and combine structural, physiognomic and functional features (e.g. arid shrublands) (Keith 2004). While they are a broad level of classification, formations provided a suitable level of discrimination for our analysis, as species' movements have been shown to be affected by habitat structure (Tischendorf and Fahrig 2000). In addition, it was more realistic to parameterise vegetation formations than the far greater number of vegetation classes, and where knowledge of species' behaviour in each class, or the ability of experts to estimate the behaviour, may be incomplete or absent. The state-wide data was clipped to the study region which reduced the number of vegetation formations from 16 to 12 and resampled from 25-m to 100-m cell resolution.

2) Vegetation condition

State-wide land-use data obtained from NSW Landuse V1 (OEH 2011). The file was clipped to the BRG catchment and contained 238 different detailed land-use descriptions. Comparison of the layer with satellite imagery revealed some inherent errors, in addition to changes to the landscape since the GIS data was collected. Scattered paddock trees were also poorly accounted for but are known to have an influence on species movement (Fischer and Lindenmayer 2002).

Two additional GIS data sets and two decision rules improved the quality of the land-use layer. The first dataset was the NSW state tenure data (OEH 2015) which updated reserves that may have been gazetted or transferred after the development of the NSW Landuse V1 data. Second, more information was sought for scattered trees. Supplementary canopy data was obtained from existing remotely-sensed foliage projective cover data (Danaher 2011). This data was constructed from SPOT 5 imagery at 5-m resolution. The data was aggregated to a 100-m cell size using the total number of 5-m cells with canopy present within each 100-m cell. The layer was converted to a binary grid, representing the presence or absence of canopy cover for each 100-m cell.

Land-use as a surrogate for vegetation condition has been used elsewhere (Doerr et al. 2013) and here we used a similar classification to reduce the number of descriptors and to make calculations more computationally tractable. Land-use classes ranged from 1 (representing the poorest vegetation condition and therefore unsuitable for native species) to 9 (best condition, found in formally protected areas). The three layers (land-use, tenure and woody canopy cover) were combined and each detailed land-use description was allocated a land-use class. Where the three layers overlapped, two decision rules were applied. First priority was given to land-use description followed by tenure, where reserves and state forests were presumed to have better habitat condition than privately owned lands (due to the potential for grazing or other modifying land-uses on private land). Reserves were presumed to have better condition than state forests (due to logging history and permissibility of grazing). Second, on private lands, priority was given to the presence of woody canopy cover (i.e. scattered trees). The presence of scattered trees was assumed to provide better habitat than their absence. Where required, the layer was compared against imagery to determine the final choice of land-use class.

The final layer was converted to a grid format with a resolution of 100 m. The land-use classes for the 238 land-use descriptions are supplied in Table S4.

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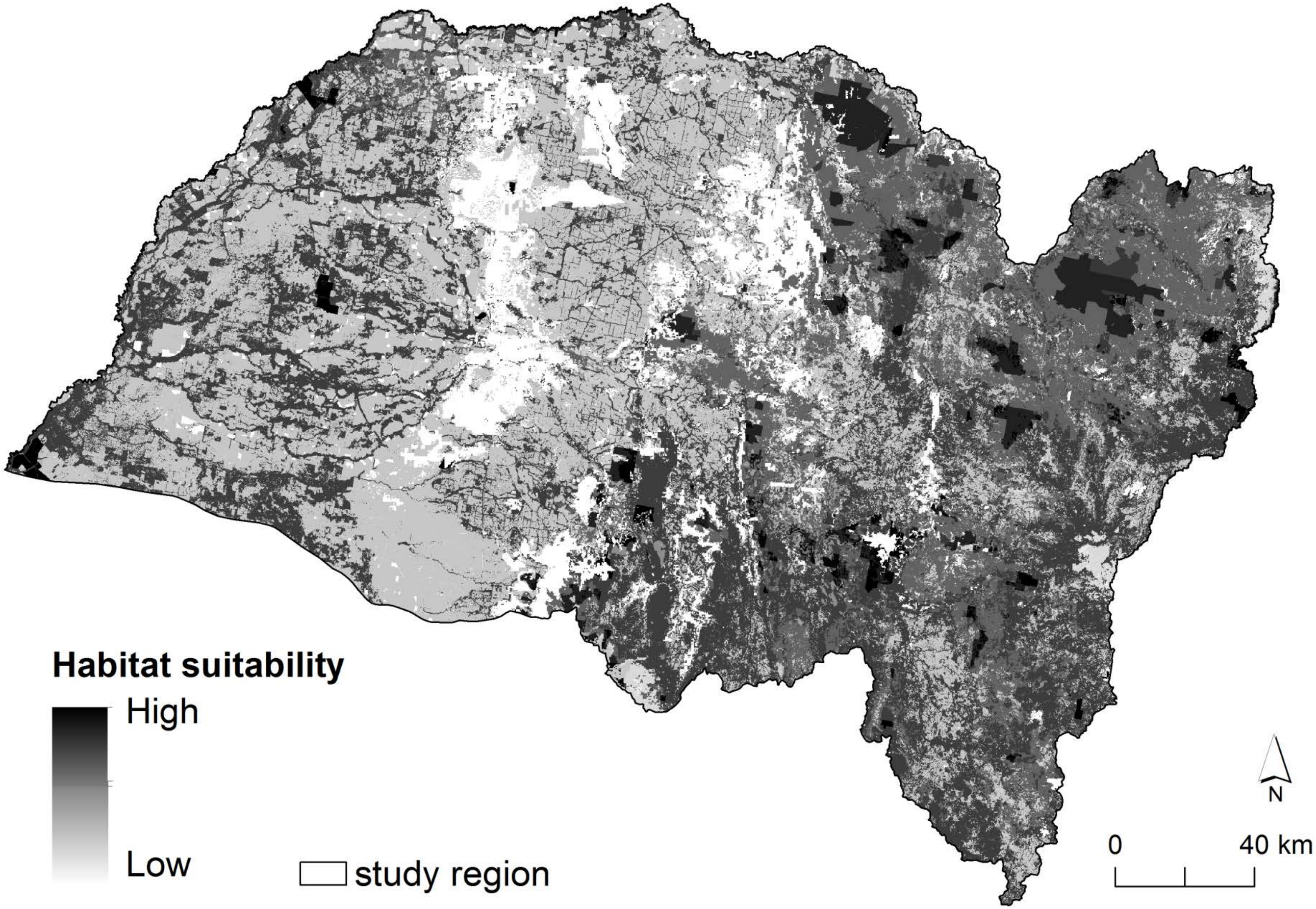
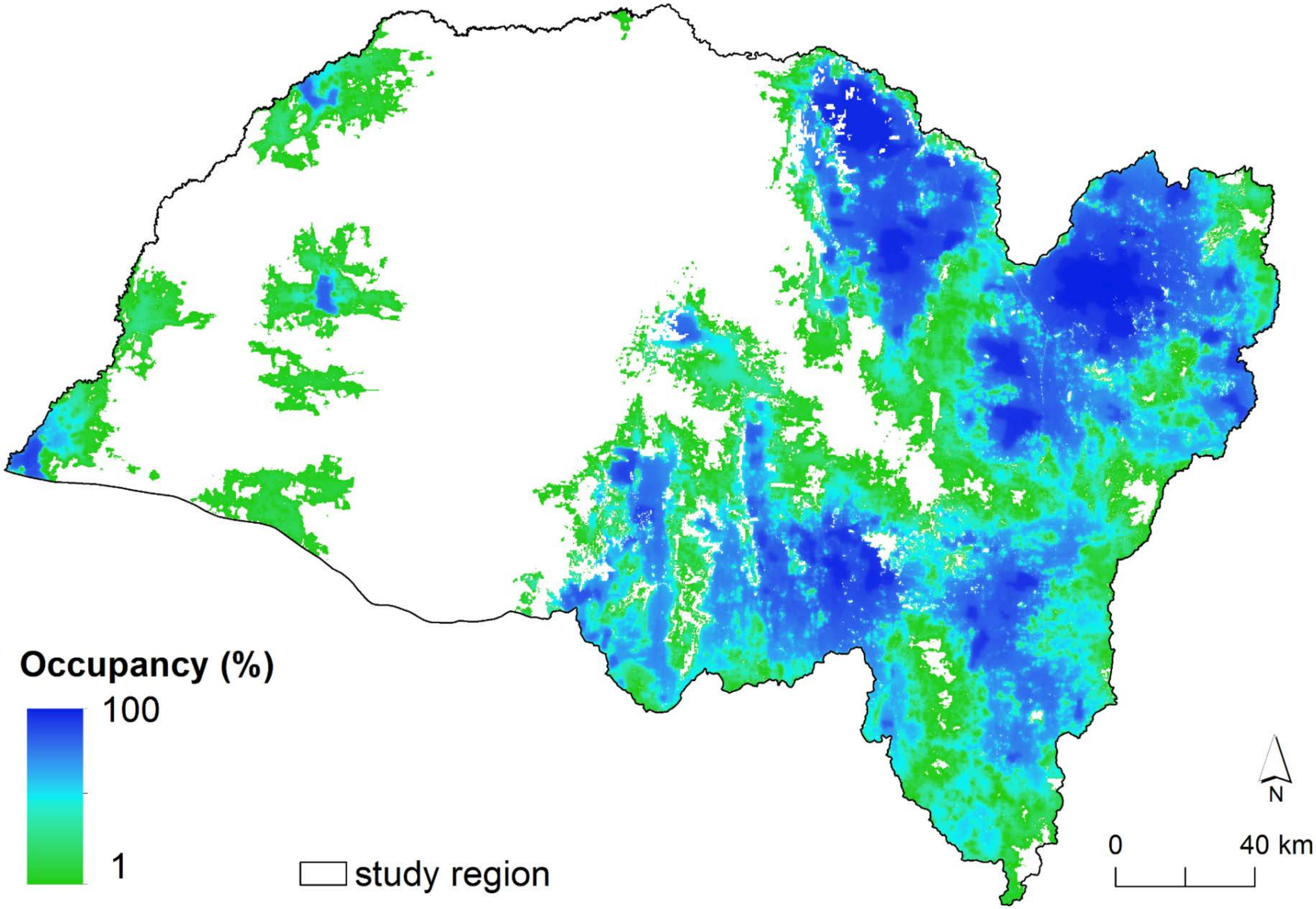
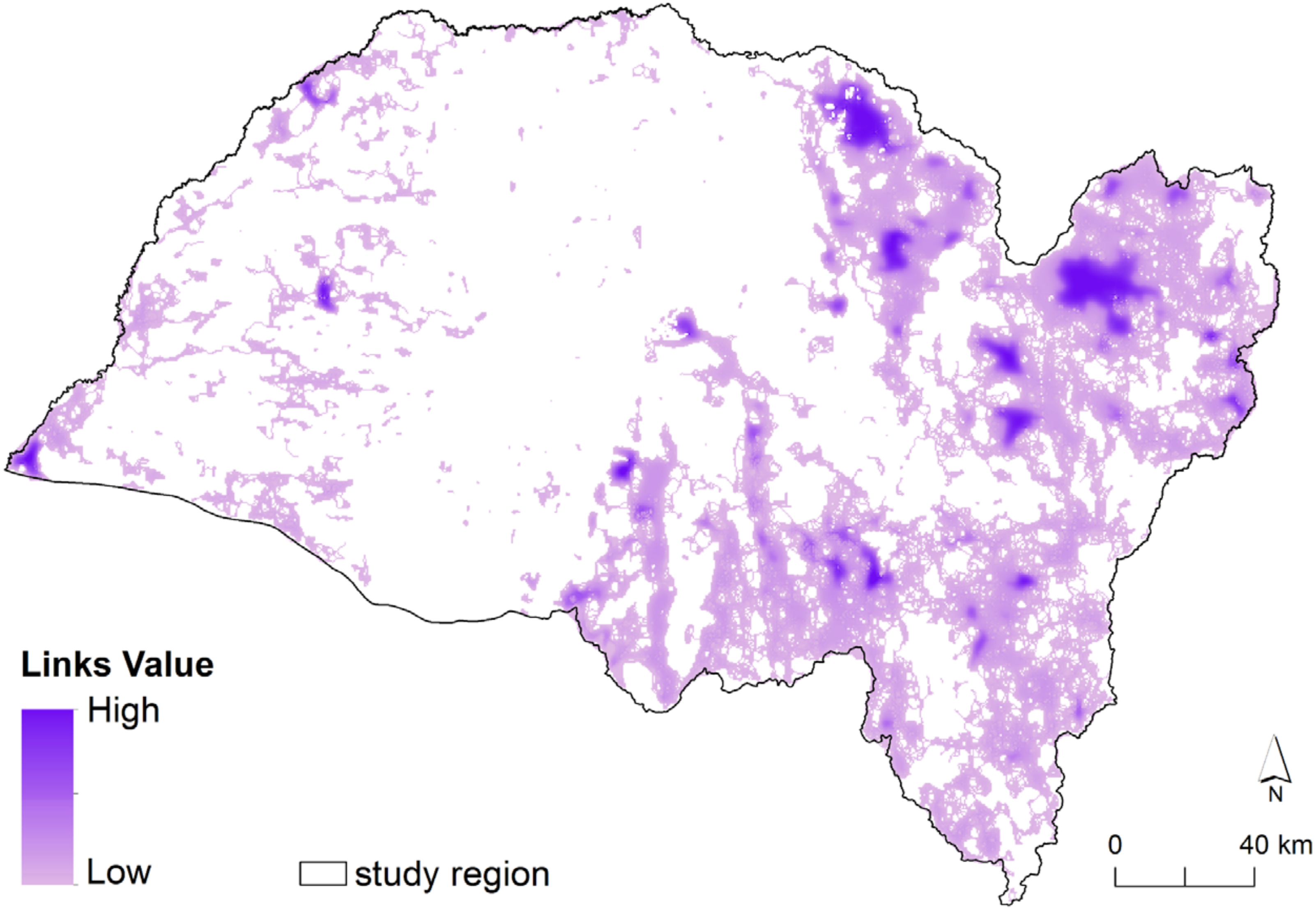
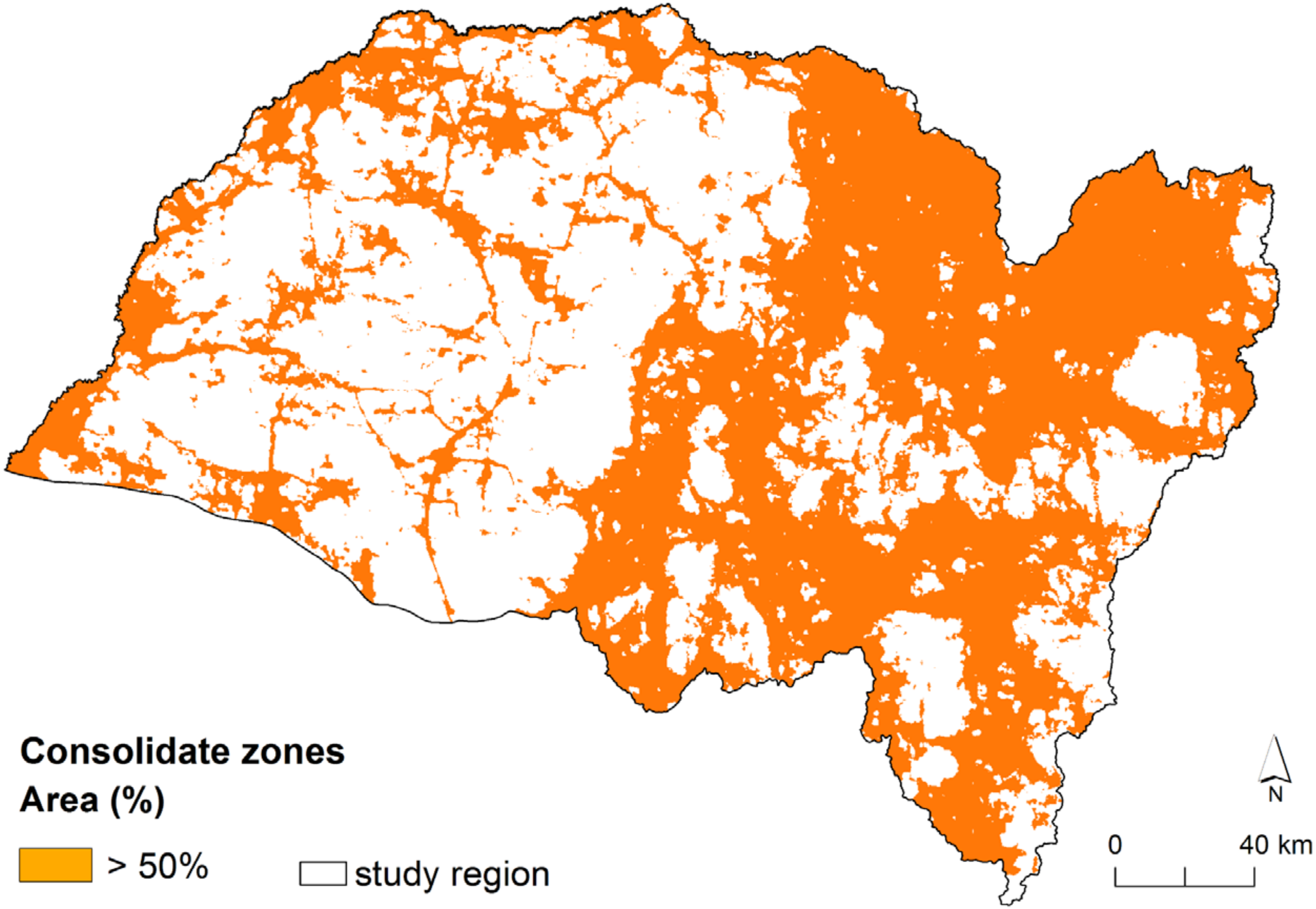
Fig. S1. Spatial outputs relating to woodland and dry forest generic focal species: a) habitat suitability; b) predicted occupancy (%) derived from REMP; c) existing dispersal pathways derived from Spatial Links Tool; d) BRG portion of state-wide Landscape Value consolidate zone mapping (top 50% of values displayed), identifying areas for habitat improvement of existing vegetation in good condition; and e) combined layers displaying occupancy (uppermost layer), existing dispersal pathways (mid-layer) and consolidate zones (bottom layer) (using colour schemes as per frames b–c). Where the existing dispersal links do not provide connections between subpopulations, connectivity can be improved through targeting restoration actions within the state-wide Landscape Value zones (top 50% of area displayed).


Habitat suitability
High
Low
study region
N
0
40 km


Occupancy (%)
100
1
study region
N
0
40 km


Links Value
High
Low
study region
N
0
40 km


Consolidate zones
Area (%)
> 50%
study region
N
0
40 km

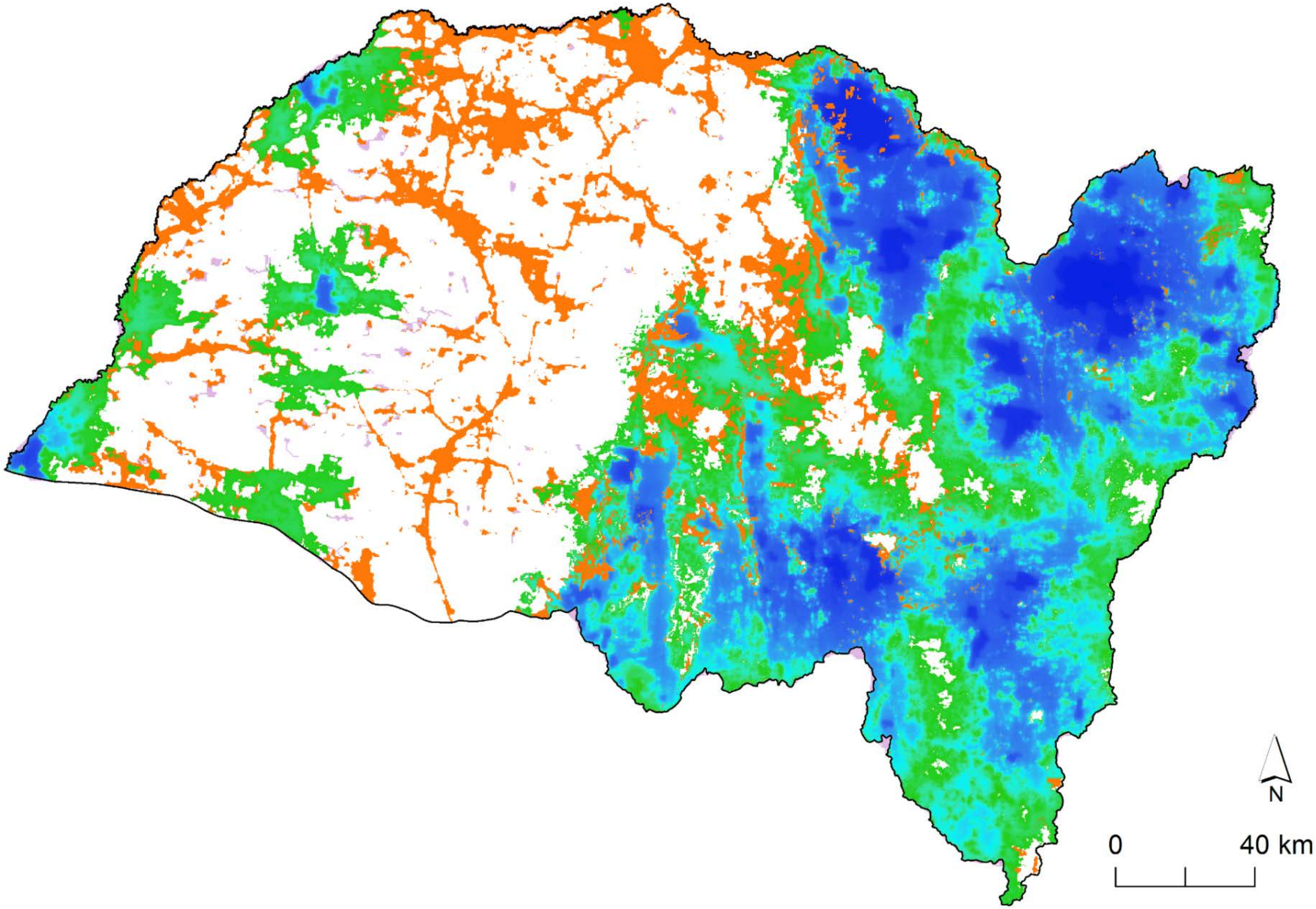

N
0
40 km

Table S1. Vegetation classification (after Keith 2004) and current extent for the Border Rivers – Gwydir catchment used in REMP–dispersal pathways analysis

Vegetation formation (and subformation)	Formation area (ha)	Proportion (%) of total area of catchment (5,079,403 ha)
Rainforests	175,599	3.46
Wet sclerophyll forests (shrubby subformation)	345	<0.01
Wet sclerophyll forests (grassy subformation)	40,893	0.81
Grassy woodlands	708,211	13.94
Grasslands	238,863	4.70
Dry sclerophyll forests (shrub/grass subformation)	555,488	10.94
Dry sclerophyll forests (shrubby subformation)	1,144,113	22.52
Heathlands	3685	0.07
Forested wetlands	18,104	0.36
Other wetlands	250	<0.01
Semi-arid woodlands (grassy subformation)	1,969,177	38.77
Semi-arid woodlands (shrubby subformation)	88,027	1.73
unknown	37,620	0.74
Total	4,980,375	98.06*

* Remaining 1.94% of catchment is cleared of vegetation

Reference

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Table S2. Parameter values used in REMP–dispersal links analysis to model woodland and dry forest GFS (taken from Doerr et al. 2013). REMP parameters are described in main text, land-use classes described in Table S3, and derivation of values described in main text

Table S2a Habitat suitability

	Habitat suitability (0–100%)						
	Land-use class						
Vegetation formation and subformation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	0	0	0	0	0	0	0
Wet sclerophyll forests (shrubby subformation)	0	4	14	4	8	18	20
Wet sclerophyll forests (grassy subformation)	0	4	14	4	8	18	20
Grassy woodlands	0	20	70	20	40	90	100
Grasslands	0	0	0	0	0	0	0
Dry sclerophyll forests (shrub/grass subformation)	0	20	70	20	40	90	100
Dry sclerophyll forests (shrubby subformation)	0	16	56	16	32	72	80
Heathlands	0	0	0	0	0	0	0
Forested wetlands	0	10	35	10	20	45	50
Other wetlands	0	10	35	10	20	45	50
Semi-arid woodlands (grassy subformation)	0	20	70	20	40	90	100
Semi-arid woodlands (shrubby subformation)	0	16	56	16	32	72	80

Table S2b Home-range movement distances

	Home-range movement distance (m)						
	Land-use class						
Vegetation formation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	25	75	150	75	200	200	200
Wet sclerophyll forests (shrubby subformation)	40	120	240	120	320	320	320
Wet sclerophyll forests (grassy subformation)	40	120	240	120	320	320	320
Grassy woodlands	50	150	300	150	400	400	400
Grasslands	10	30	60	30	80	80	80
Dry sclerophyll forests (shrub/grass subformation)	50	150	300	150	400	400	400
Dry sclerophyll forests (shrubby subformation)	50	150	300	150	400	400	400
Heathlands	10	30	60	30	80	80	80
Forested wetlands	40	120	240	120	320	320	320
Other wetlands	40	120	240	120	320	320	320
Semi-arid woodlands (grassy subformation)	50	150	300	150	400	400	400
Semi-arid woodlands (shrubby subformation)	50	150	300	150	400	400	400

Table S2c Dispersal movement distances

	Dispersal movement distance (m)						
	Land-use class						
Vegetation formation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	50	200	1,650	750	1,650	1,650	1,650
Wet sclerophyll forests (shrubby subformation)	80	320	2,640	1,200	2,640	2,640	2,640
Wet sclerophyll forests (grassy subformation)	80	320	2,640	1,200	2,640	2,640	2,640
Grassy woodlands	100	400	3,300	1,500	3,300	3,300	3,300
Grasslands	20	80	660	300	660	660	660
Dry sclerophyll forests (shrub/grass subformation)	100	400	3,300	1,500	3,300	3,300	3,300
Dry sclerophyll forests (shrubby subformation)	100	400	3,300	1,500	3,300	3,300	3,300
Heathlands	20	80	660	300	660	660	660
Forested wetlands	80	320	2,640	1,200	2,640	2,640	2,640
Other wetlands	80	320	2,640	1,200	2,640	2,640	2,640
Semi-arid woodlands (grassy subformation)	100	400	3,300	1,500	3,300	3,300	3,300
Semi-arid woodlands (shrubby subformation)	100	400	3,300	1,500	3,300	3,300	3,300

Reference

Doerr V, Williams K, Drielsma M et al. (2013) Designing landscapes for biodiversity under climate change Final Report. National Climate Change Adaptation Research Facility, Gold Coast, Queensland

Keith DA (2004) Ocean shores to desert dunes: the native vegetation of New South Wales and the ACT. Department of Environment and Conservation (NSW), Hurstville, NSW

Table S3. Land-use classes used as surrogates for vegetation condition (adapted from Doerr et al. 2013). N.B. Numbering of land-use classes is not consecutive but does not affect analysis

Vegetation condition	Land-use class	Description
Poorest	1	Non-habitat for natives, areas devoid of native vegetation (e.g. urban area, open water, bare areas, roads and other infrastructure).
	2	Crops and pastures with no trees, heavily modified from natural systems and managed for non-woody production (e.g. grassy crops, improved pasture, partially natural pastures without scattered trees).
	3	Crops and pastures with scattered trees and managed for non-woody production (e.g. partially natural pastures, margins of private native remnants, private semi-developed bush blocks).
	4	Woody production or heavily modified native ecosystems (e.g. single species

		plantations, perennial horticulture).
	5	Environmental plantings, natural regrowth and areas planted with native tree species (e.g. revegetation of native vegetation).
	8	Modified native woody ecosystems, partially to mostly intact native ecosystems on state-owned lands (e.g. natural areas under non-perpetual stewardship or management agreements, state native forest (logged and/or grazed).
Best	9	Native ecosystems that are formally protected and mostly intact native ecosystems with formal protection status (e.g. national parks, in-perpetuity conservation agreements).

Reference

Doerr V, Williams K, Drielsma M et al. (2013) Designing landscapes for biodiversity under climate change: final report. National Climate Change Adaptation Research Facility, Gold Coast, Queensland

Table S4. Land-use descriptions and associated classes for land-use grid data used in REMP–dispersal pathways analysis. Land-use descriptions taken from Landuse V1 (OEH 2011). Land-use classes are described in Table S3 with further qualification from land tenure and woody canopy layers. For example, a polygon of the class "native or improved pasture within a State Forest" may also have had woody canopy present. In this case, the land-use-class was recorded as 3; if no canopy present, the land-use class was recorded as 8

Land-use description	Land-use class
Abandoned orchard and vine lands; trees/vines not maintained and may be dying; regrowth of native shrubs and trees is occurring	5
Abandoned urban or industrial area and site is locked up e.g. Glen Alice	1
Abattoir	1
Aerodrome/airport	1
Agricultural industry in a rural location e.g. cotton gin (See also class 53.)	2
Agro forestry	2
Airstrip (local/farmer, grass or bare surface, not sealed)	1
Ancillary (saddle) wall to reservoir	1
Aquaculture - fish, prawn, yabby or beach worm farm	1
Area recently under development for urban, commercial and/or industrial uses - infrastructure in place but no building activity	1

Areas irrigated with effluent from sewage disposal ponds	1
Areas of dense standing dead trees with the ground cover consisting of volunteer species such as bracken, blady grass and tea tree	2 or 3
Beach	1
Bore drain (active)	1 or 3
Building associated with horticultural industry (winery, packing shed)	1
Caravan park or mobile home village	1
Cemetery	1
Cliff/rock outcrop	1
Communications facility	1
Constructed grass waterway for water disposal. Part of a soil erosion control system carrying run-off from graded banks	2 or 3
Constructed wetland for conservation or water improvement	8
Cotton	2
Cotton - irrigated	2
Cotton - irrigated; irrigation practice - laser levelled with tail water reticulation and on-farm storage of tail water	2
Cropping - continuous or rotation	2

Cropping - continuous or rotation - irrigated	2 or 3
Cropping - continuous or rotation - irrigated; irrigation practice - centre pivot	2 or 3
Cropping - continuous or rotation - irrigated; irrigation practice - laser levelled with tail water reticulation and on-farm storage of tail water	2 or 3
Cropping - continuous or rotation - with a woody vegetation cover of woodland	2 or 3
Cropping - continuous or rotation within a State Forest	2 or 9
Cropping - with a fixed irrigation system not used at the time of mapping	2 or 3
Cropping of legumes for seed - chickpeas, lupins, vetches, field beans	2 or 3
Cropping within an ephemeral wetland - with a woody vegetation cover of woodland	2 or 3
Cropping within an ephemeral wetland (does not include cropping within an ephemeral lake - see classes 186 & 187)	2 or 3
Cropping within bed of an ephemeral lake; lake is not regulated or above regulation level	2 or 3
Cropping within controlled flood system; prohibition on the construction of barriers to the movement of water	2 or 3
Crown reserve	9
Crown reserve with public access	9
Cultural heritage site - aboriginal or European	9

Defence facility	1
Degraded land (salt site, eroded area)	1 or 2
Degraded land (salt site, eroded area) within a State Forest	1
Dense shrub growth - limited to nil grazing capacity	5
Derelict mining land	1
Derelict mining land within a State Forest	1
Derelict mining land, previously used for sapphire mining	1
Derelict mining land, previously used for tin mining	1
Disposal dam, depression or lake bed for irrigation tail water	1 or 3
Drainage channel (from irrigation system or a channel draining a swamp; base of channel is lined)	1
Drainage depression in cropping paddock	2 or 3
Drainage depression in cropping paddock - with a woody vegetation cover of woodland	2 or 3
Drainage depression in cropping paddock - with more than 30% of ground area having regeneration of native tree species	2 or 3
Drainage or water supply channel - base of channel is not lined	1
Effluent ponds from intensive animal industries	1

Electricity generation (power station and associated stockpiles, hydro-electric plants	1
Electricity substation	1
Energy corridor	1
Energy corridor within a State Forest	1
Eucalyptus oil plantation	4
Farm dam	1
Farm Infrastructure - house, machinery & storage sheds and garden areas	1
Firebreak	2 or 3
Flood chute (flood runners that are filled with water during and after floods) and designated floodway in irrigation districts, localities	2 or 3
Flood chute in irrigation districts, localities - with a woody vegetation cover of woodland	3
Flood or irrigation structure	1
Flood refuge (constructed features located within flood prone areas)	2 or 3
Flood runners in western NSW - with more than 30% of ground area having regeneration of native tree species	3
Flood runners in western NSW. (Vegetation is indicative of a more prolonged period of inundation or wetness)	2 or 3

Floodplain swamp	2 or 3
Floodplain swamp - back swamp	2 or 3
Floodplain swamp - billabong	2 or 3
Floodplain swamp - with a woody vegetation cover of open forest	2
Floodplain swamp - with a woody vegetation cover of woodland	2 or 3
Fly ash dam/spoil dump	1
Fly ash dam/spoil dump, previously used for sapphire mining	1
Fodder crop	2 or 3
Fodder crop - irrigated	2 or 3
Fodder crop - with a fixed irrigation system not used at the time of mapping	2 or 3
Foreshores land to State Water dam	9
Government and private facilities - gaol, training centre, school, religious institutions & training centres, religious retreats	1
Grassland within mining lease	3
Grazing - Residual strips (block or linear feature) of native grassland within cultivated paddock - with a woody vegetation cover of open forest	2 or 3

Grazing - Residual strips (block or linear feature) of native grassland within cultivated paddock - with a woody vegetation cover of woodland	2 or 3
Grazing - Residual strips (block or linear feature) of native grassland within cultivated paddock. Strips contain scattered to isolated trees only	2 or 3
Grazing - Residual strips (block or linear feature) of native grassland within cultivated paddock. Strips contain scattered to isolated trees only - with more than 30% of ground area having native shrub regeneration.	3
Grazing of native vegetation. Grazing of domestic stock on essentially unmodified native vegetation	2 or 3
Grazing of native vegetation. Grazing of domestic stock on essentially unmodified native vegetation - with a woody vegetation cover of open forest	2 or 3
Grazing of native vegetation. Grazing of domestic stock on essentially unmodified native vegetation - with a woody vegetation cover of woodland	2 or 3
Grazing of native vegetation. Grazing of domestic stock on essentially unmodified native vegetation - with more than 30% of ground area having native shrub regeneration	2 or 3
Grazing of native vegetation. Grazing of domestic stock on essentially unmodified native vegetation - with more than 30% of ground area having regeneration of native tree species	2 or 3

Grazing of native vegetation. Grazing of domestic stock on essentially unmodified native vegetation, with previous evidence of cultivation	2 or 3
Grazing of riparian land	2 or 3
Grazing of riparian land - with a woody vegetation cover of open forest	3
Grazing of riparian land - with a woody vegetation cover of woodland	3
Grazing of salt affected land	2 or 3
Grazing within an ephemeral wetland - with a woody vegetation cover of closed forest	2 or 3
Grazing within an ephemeral wetland - with a woody vegetation cover of open forest	2 or 3
Grazing within an ephemeral wetland - with a woody vegetation cover of woodland	2 or 3
Grazing within an ephemeral wetland - with more than 30% of ground area having native shrub regeneration	2 or 3
Grazing within an ephemeral wetland - with more than 30% of ground area having regeneration of native tree species	3
Grazing within an ephemeral wetland (does not include cropping within an ephemeral lake - see classes 182 & 189)	2 or 3
Grazing within bed of an ephemeral lake or watercourse; lake or watercourse are not regulated or above regulation level	2
Grazing within bed of an ephemeral lake or watercourse; lake or watercourse are not regulated or above regulation level with a dense shrub or tree cover	2 or 3

Hobby farm (as distinct from rural residential. Small, single blocks no longer used for rural purposes	1
Horse stud and/or horse breeding facilities	1
Industrial/commercial	1
Intensive animal production	1
Intensive animal production - beef feedlot	1
Intensive animal production - ostriches	1
Intensive animal production - piggery	1
Intensive animal production - sheep	1
Irrigated pastures	2
Irrigation dam	1
Irrigation farm infrastructure; miscellaneous lands within farms including access roads, bund walls, buildings and services	1
Irrigation farm infrastructure; miscellaneous lands within farms including access roads, bund walls, buildings and services - with a woody vegetation cover of woodland	1
Irrigation farm infrastructure; miscellaneous lands within farms including access roads, bund walls, buildings and services - with more than 30% of ground area having native shrub regeneration	1

Irrigation farm infrastructure; miscellaneous lands within farms including access roads, bund walls, buildings and services - with more than 30% of ground area having regeneration of native tree species	1
Irrigation from abattoir and other industry	1
Irrigation supply channel	1
Jojoba planting	4
Lagoon or inland lake	1
Land fenced for riparian management	9
Land vested with an aboriginal land council	8
Landfill (garbage)	1
Lands fenced and treated for land degradation problems	1
Lantana, blackberry and other exotic weed infested grazing land	2
Levee bank for urban area	1
Levee for flood protection around house and farm infrastructure	1
Mine site	1
Mine site, used for sapphire mining	1

National park	9
Native forest	2 or 3
Native forest - regeneration	5
Native forest - regeneration and within a State Forest	5
Native forest and within a State Forest	8
Native shrub plantation (eg tea tree)	4
Native woody shrub	3
Native woody species - regeneration comprising shrub or understorey species	5
Nature reserve	9
No identified use	1
Nursery	1
Olives	4
Olives - irrigated	4
Orchard - tree fruits	4
Orchard - tree fruits - irrigated	4

Orchard - tree fruits - irrigated; irrigation practice - laser levelled with tail water reticulation and on-farm storage of tail water	4
Oyster spoil & sheds, but not submerged leases	1
Pecan, macadamia and other nuts - irrigated	4
Pine plantation - previously used for mining or quarrying activity	4
Prior stream	2 or 3
Prior stream - with a woody vegetation cover of open forest	3
Prior stream - with a woody vegetation cover of woodland	2 or 3
Private conservation agreement	8
Protected area managed for conservation of specific natural features - with more than 30% of ground area having regeneration of native tree species	8
Protected area managed for conservation of specific natural features.	8
Pump site, urban or irrigation supply	1
Quarry	1
Quarry - within a State Forest	1
Railway	1

Railway - track no longer used	1
Rangeland grazing	3
Rangeland grazing - with a woody vegetation cover of woodland	3
Recently cleared land (cleared of forest vegetation as yet not covered by crop or pasture)	2
Recently cleared land (cleared of forest vegetation as yet not covered by crop or pasture) - with more than 30% of ground area having regeneration of native tree species	2
Regeneration within sites cleared under a 'window-pane' pattern	2
Research facility	1
Reservoir	1
Residential	1
Resort style private land use	1
Restored mining lands	5
Restored mining lands, previously used for sapphire mining	5
Restored mining lands, previously used for tin mining	5
Riparian vegetation - exotic species (principally willow)	4

River and riparian vegetation where the river channel is filled by more than 50% of phragmites or cumbungi	1
River gravel deposit	1
River training work	1
River, creek or other incised drainage feature within a State Forest; includes cowals in western NSW	8
River, creek or other incised drainage feature; includes cowals in western NSW	1
River, creek or other incised drainage feature; includes cowals in western NSW - with a woody vegetation cover of woodland	3
Road or road reserve	1
Road or road reserve - with a woody vegetation cover of woodland	3
Road or road reserve within a State Forest	8
Rural recreation. Blocks are isolated and not associated with an urban area	3
Rural residential	1
Saleyard	1
Salt treatment or salt demonstration site (discharge and recharge sites)	2
Saltbush plantings (for grazing purposes and not as part of a salinity control programme)	4
Sawmill	1

Secondary grassland in forested areas	3
Sewage disposal ponds	1
Shade house or glass house (includes hydroponic use)	1
Small to medium forested or wilderness blocks with isolated residential buildings. (Rural residential but the forested or wilderness feature of the block is worth noting.)	2 or 8
Softwood plantation	4
Softwood plantation - nursery	1
Softwood plantation and within a State Forest	4
Sown, improved pastures - with fixed irrigation system not used at the time of mapping	2
Sown, improved perennial pastures	2 or 3
Sown, improved perennial pastures - with a woody vegetation cover of open forest	3
Sown, improved perennial pastures - with a woody vegetation cover of woodland	3
State forest	8
State recreation area	9
Stock pile of mined material, located remotely from mine site. Often situated next to railway lines or at ports	1

Storage site for agricultural chemicals and products (e.g. fertiliser dumps, cotton bunkers and temporary grain storages)	1
Swamp	1 or 3
Temporary water storage area (e.g. rice farming - opportunistic storage of water in natural depressions	1
Tourist development	1
Tree lot	4
Tree lot - exotic species	4
Turf farming	1
Turf farming - irrigated	1
University or other tertiary institution	1
Urban recreation	1
Urban recreation - irrigated	1
Vegetables	1
Vegetables - irrigated	1
Vineyard - grape and other vine fruits	4
Vineyard - grape and other vine fruits - irrigated	4

Volunteer, naturalised or improved pastures - with a woody vegetation cover of closed forest	3
Volunteer, naturalised or improved pastures - with a woody vegetation cover of open forest	2 or 3
Volunteer, naturalised or improved pastures - with a woody vegetation cover of woodland	2 or 3
Volunteer, naturalised, native or improved pastures	2 or 3
Volunteer, naturalised, native or improved pastures - with fixed irrigation system not used at the time of mapping	2 or 3
Volunteer, naturalised, native or improved pastures - with more than 30% of ground area having exotic weeds	2 or 3
Volunteer, naturalised, native or improved pastures - with more than 30% of ground area having native shrub regeneration	2 or 3
Volunteer, naturalised, native or improved pastures - with more than 30% of ground area having regeneration of native tree species	2 or 3
Volunteer, naturalised, native or improved pastures - with more than 30% of ground area having regeneration of native tree species and within a State Forest	8
Volunteer, naturalised, native or improved pastures within a State Forest	3 or 8
Volunteer, naturalised, native or improved pastures, with previous evidence of cultivation	2 or 3
Water supply pressure reservoir including water filtration plant	1
Wide road reserve or TSR, currently used for intensive grazing	2 or 3

Wide road reserve or TSR, heavily timbered but with some grazing	2 or 3
Wide road reserve or TSR, with some grazing	2 or 3
Wide road reserve or TSR, with some grazing - with a woody vegetation cover of open forest	3
Wide road reserve or TSR, with some grazing - with a woody vegetation cover of woodland	2 or 3
Wide road reserve or TSR, with some grazing - with more than 30% of ground area having native shrub regeneration	2 or 3
Wide road reserve or TSR, with some grazing - with more than 30% of ground area having regeneration of native tree species	2 or 3
Windbreak or tree corridor	5
Windbreak or tree corridor - with more than 30% of ground area having regeneration of native tree species	5

Reference

OEH (Office of Environment and Heritage) (2011) New South Wales land use mapping project. LanduseV1 created 2007, updated 2011. Sydney, NSW

Appendix 3

Appendix S1. Methods

Compilation of fauna dataset for REMP model evaluation

Presence records were sourced from the Atlas of NSW Wildlife, Office of Environment and Heritage (OEH, 2015) using the following criteria:

- All fauna species for the geographical location Border Rivers–Gwydir Catchment Management Authority
- Only records post-2005 were sourced, as older records may be associated with vegetation that has been cleared since submission of the record. This date is after the introduction of the new NSW *Native Vegetation Act 2004* and it was assumed habitat had a greater chance of currently being extant. This was checked against the vegetation extent layer used in the REMP modelling and where records were situated within the category 'cleared', the record was deleted
- Records with 300 m or greater accuracy
- Species names as per Table 1 in the main text were used. The Atlas can be accessed at http://www.bionet.nsw.gov.au/ (last accessed May 2015)

These data was further "cleaned" to retain only records originating from either a systematic method or systematic survey programme, according to the following criteria:

- Systematic surveys were determined from the 'DatasetName' or 'SurveyName' fields (e.g. Wildcount, other survey name, BirdsAustralia, OEH Data from Scientific Licences dataset), or which were obtained from a recognised survey technique from the 'TechniqueType' (e.g. pitfalls, mist-netting, trapped, diurnal herpetofauna searches)

- No opportunistic records, as determined from entries under ‘Description’, ‘LocationNotes’, ‘TechniqueType’ or ‘SightingNotes’ fields

If the origins of the record were unclear, the recorded observer was contacted for clarification (if possible); otherwise, the record was removed.

Additionally, records that were considered part of a target species programme were removed, as there was no guarantee systematic searches for other species had occurred at these locations. These deleted records were for frogs, turtles, fish, bats, koalas and quolls. Exotic species records were also deleted.

The final dataset comprised 11,276 individual species records extracted from the original 139,749 records. These records occurred across 917 geographic locations (i.e. unique geographic coordinate locations).

Appendix S2. Tables and Figures

Table S1. Vegetation classification (after Keith 2004) and current extent for the Border Rivers – Gwydir catchment used in REMP analysis

Code	Vegetation formation (and subformation)	Formation area (ha)	Proportion (%) of area of study region (5,079,403 ha)
1	Rainforests	175,599	3.46
2	Wet sclerophyll forests (shrubby subformation)	345	<0.01
3	Wet sclerophyll forests (grassy subformation)	40,893	0.81
4	Grassy woodlands	708,211	13.94
5	Grasslands	238,863	4.70
6	Dry sclerophyll forests (shrub/grass subformation)	555,488	10.94
7	Dry sclerophyll forests (shrubby subformation)	1,144,113	22.52
8	Heathlands	3685	0.07
10	Forested wetlands	18,104	0.36
11	Other wetlands	250	<0.01
12	Semi-arid woodlands (grassy subformation)	1,969,177	38.77
13	Semi-arid woodlands (shrubby subformation)	88,027	1.73
	unknown	37,620	0.74
	Total	4,980,375	98.06*

* Remaining 1.94% of catchment is cleared of vegetation

Table S2. Parameter values used in REMP analysis to model two parameterisations of woodland and dry forest GFS (taken from Doerr et al. 2013). REMP parameters, land-use classes, and derivation of values are described in Foster et al. (2017). GFS1 and GFS2 differ in the parameter thresholds.

Dry woodland and forest species generic GFS1 (25th percentile values for movement distances, and 25th percentile for minimum viable habitat)

Table S2a Habitat suitability

	Habitat (H) suitability (0–100%)						
	Land-use class						
Vegetation formation and subformation (after Keith 2004)	1	2	3	4	5	8	9
Rainforests	0	0	0	0	0	0	0
Wet sclerophyll forests (shrubby subformation)	0	4	14	4	8	18	20
Wet sclerophyll forests (grassy subformation)	0	4	14	4	8	18	20
Grassy woodlands	0	20	70	20	40	90	100
Grasslands	0	0	0	0	0	0	0
Dry sclerophyll forests (shrub/grass subformation)	0	20	70	20	40	90	100
Dry sclerophyll forests (shrubby subformation)	0	16	56	16	32	72	80
Heathlands	0	0	0	0	0	0	0
Forested wetlands	0	10	35	10	20	45	50
Other wetlands	0	10	35	10	20	45	50
Semi-arid woodlands (grassy subformation)	0	20	70	20	40	90	100
Semi-arid woodlands (shrubby subformation)	0	16	56	16	32	72	80

Table S2b Home-range movement distances

	Home-range (P) movement distance (m)						
	Land-use class						
Vegetation formation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	25	75	150	75	200	200	200
Wet sclerophyll forests (shrubby subformation)	40	120	240	120	320	320	320
Wet sclerophyll forests (grassy subformation)	40	120	240	120	320	320	320
Grassy woodlands	50	150	300	150	400	400	400
Grasslands	10	30	60	30	80	80	80
Dry sclerophyll forests (shrub/grass subformation)	50	150	300	150	400	400	400
Dry sclerophyll forests (shrubby subformation)	50	150	300	150	400	400	400
Heathlands	10	30	60	30	80	80	80
Forested wetlands	40	120	240	120	320	320	320
Other wetlands	40	120	240	120	320	320	320
Semi-arid woodlands (grassy subformation)	50	150	300	150	400	400	400
Semi-arid woodlands (shrubby subformation)	50	150	300	150	400	400	400

Table S2c Dispersal movement distances

	Dispersal (DP) movement distance (m)						
	Land-use class						
Vegetation formation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	50	200	1650	750	1650	1650	1650
Wet sclerophyll forests (shrubby subformation)	80	320	2640	1200	2640	2640	2640
Wet sclerophyll forests (grassy subformation)	80	320	2640	1200	2640	2640	2640
Grassy woodlands	100	400	3300	1500	3300	3300	3300
Grasslands	20	80	660	300	660	660	660
Dry sclerophyll forests (shrub/grass subformation)	100	400	3300	1500	3300	3300	3300
Dry sclerophyll forests (shrubby subformation)	100	400	3300	1500	3300	3300	3300
Heathlands	20	80	660	300	660	660	660
Forested wetlands	80	320	2640	1200	2640	2640	2640
Other wetlands	80	320	2640	1200	2640	2640	2640
Semi-arid woodlands (grassy subformation)	100	400	3300	1500	3300	3300	3300
Semi-arid woodlands (shrubby subformation)	100	400	3300	1500	3300	3300	3300

Table 2d Parameters that apply across all vegetation formations and land uses, including grid cell sizes relevant to resource utilisation (SC_CS) and dispersal (LC_CS) as well as minimum viable habitat area (MVH)

Entity name	SC_CS (m)	H min (%)	H max (%)	P min (m)	P max (m)	LC_CS (m)	MVH (ha)	DP min (m)	DP max (m)
GFS1	100	0	100	10	400	400	1100	20	3300

Dry woodland and forest species generic GFS2 (median values for movement distances and 25th percentile for minimum viable habitat)

Table S2e Habitat suitability

	Habitat (H) suitability (0–100%)						
	Land-use class						
Vegetation formation and subformation (after Keith 2004)	1	2	3	4	5	8	9
Rainforests	0	0	0	0	0	0	0
Wet sclerophyll forests (shrubby subformation)	0	5	16	5	9	19	20
Wet sclerophyll forests (grassy subformation)	0	5	16	5	9	19	20
Grassy woodlands	0	25	80	25	45	95	100
Grasslands	0	0	0	0	0	0	0
Dry sclerophyll forests (shrub/grass subformation)	0	25	80	25	45	95	100
Dry sclerophyll forests (shrubby subformation)	0	20	64	20	36	76	80
Heathlands	0	0	0	0	0	0	0
Forested wetlands	0	13	40	13	23	48	50
Other wetlands	0	13	40	13	23	48	50
Semi-arid woodlands (grassy subformation)	0	25	80	25	45	95	100
Semi-arid woodlands (shrubby subformation)	0	20	64	20	36	76	80

Table S2f Home-range movement distances

	Home-range (P) movement distance (m)						
	Land-use class						
Vegetation formation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	25	100	200	100	250	250	250
Wet sclerophyll forests (shrubby subformation)	40	160	320	160	400	400	400
Wet sclerophyll forests (grassy subformation)	40	160	320	160	400	400	400
Grassy woodlands	50	200	400	200	500	500	500
Grasslands	10	40	80	40	100	100	100
Dry sclerophyll forests (shrub/grass subformation)	50	200	400	200	500	500	500
Dry sclerophyll forests (shrubby subformation)	50	200	400	200	500	500	500
Heathlands	10	40	80	40	100	100	100
Forested wetlands	40	160	320	160	400	400	400
Other wetlands	40	160	320	160	400	400	400
Semi-arid woodlands (grassy subformation)	50	200	400	200	500	500	500
Semi-arid woodlands (shrubby subformation)	50	200	400	200	500	500	500

Table S2g Dispersal movement distances

	Dispersal (DP) movement distance (m)						
	Land-use class						
Vegetation formation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	50	300	2400	1000	2400	2400	2400
Wet sclerophyll forests (shrubby subformation)	80	480	3840	1600	3840	3840	3840
Wet sclerophyll forests (grassy subformation)	80	480	3840	1600	3840	3840	3840
Grassy woodlands	100	600	4800	2000	4800	4800	4800
Grasslands	20	120	960	400	960	960	960
Dry sclerophyll forests (shrub/grass subformation)	100	600	4800	2000	4800	4800	4800
Dry sclerophyll forests (shrubby subformation)	100	600	4800	2000	4800	4800	4800
Heathlands	20	120	960	400	960	960	960
Forested wetlands	80	480	3840	1600	3840	3840	3840
Other wetlands	80	480	3840	1600	3840	3840	3840
Semi-arid woodlands (grassy subformation)	100	600	4800	2000	4800	4800	4800
Semi-arid woodlands (shrubby subformation)	100	600	4800	2000	4800	4800	4800

Table 2h Parameters that apply across all vegetation formations and land uses, including grid cell sizes relevant to resource utilisation (SC_CS) and dispersal (LC_CS) as well as minimum viable habitat area (MVH)

Entity name	SC_CS (m)	H min (%)	H max (%)	P min (m)	P max (m)	LC_CS (m)	MVH (ha)	DP min (m)	DP max (m)
GFS2	100	0	100	10	500	500	1100	20	4800

Table S3. Expert-derived parameter values used in REMP analysis to model brown treecreeper. REMP parameters and land-use classes are described in (Foster et al. 2017).

Table S3a Habitat suitability

	Habitat (H) suitability (0–100%)						
	Land-use class						
Vegetation formation and subformation (after Keith 2004)	1	2	3	4	5	8	9
Rainforests	`0	0	0	0	0	0	0
Wet sclerophyll forests (shrubby subformation)	0	0	0	0	0	0	0
Wet sclerophyll forests (grassy subformation)	0	0	0	0	0	0	0
Grassy woodlands	0	10	50	10	90	100	100
Grasslands	0	0	0	0	0	0	0
Dry sclerophyll forests (shrub/grass subformation)	0	10	50	10	90	100	100
Dry sclerophyll forests (shrubby subformation)	0	8	40	8	72	80	80
Heathlands	0	0	0	0	0	0	0
Forested wetlands	0	7	35	7	63	70	70
Other wetlands	0	0	0	0	0	0	0
Semi-arid woodlands (grassy subformation)	0	10	50	10	90	100	100
Semi-arid woodlands (shrubby subformation)	0	7	53	7	63	70	70

Table S3b Home-range movement distances

	Home-range (P) movement distance (m)						
	Land-use class						
Vegetation formation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	10	10	50	20	50	100	100
Wet sclerophyll forests (shrubby subformation)	10	10	50	20	50	100	100
Wet sclerophyll forests (grassy subformation)	10	10	50	20	50	100	100
Grassy woodlands	50	50	250	100	250	500	500
Grasslands	10	10	50	20	50	100	100
Dry sclerophyll forests (shrub/grass subformation)	50	50	250	100	250	500	500
Dry sclerophyll forests (shrubby subformation)	45	45	225	90	225	450	450
Heathlands	10	10	50	20	50	100	100
Forested wetlands	40	40	200	80	200	400	400
Other wetlands	10	10	50	20	50	100	100
Semi-arid woodlands (grassy subformation)	50	50	250	100	250	500	500
Semi-arid woodlands (shrubby subformation)	40	40	200	80	200	400	400

Table S3c Dispersal movement distances

	Dispersal (DP) movement distance (m)						
	Land-use class						
Vegetation formation (Keith 2004)	1	2	3	4	5	8	9
Rainforests	20	40	700	700	700	700	700
Wet sclerophyll forests (shrubby subformation)	20	40	700	700	700	700	700
Wet sclerophyll forests (grassy subformation)	20	40	700	700	700	700	700
Grassy woodlands	100	200	3500	3500	3500	3500	3500
Grasslands	20	40	700	700	700	700	700
Dry sclerophyll forests (shrub/grass subformation)	100	200	3500	3500	3500	3500	3500
Dry sclerophyll forests (shrubby subformation)	90	180	3150	3150	3150	3150	3150
Heathlands	20	40	700	700	700	700	700
Forested wetlands	80	160	2800	2800	2800	2800	2800
Other wetlands	20	40	700	700	700	700	700
Semi-arid woodlands (grassy subformation)	100	200	3500	3500	3500	3500	3500
Semi-arid woodlands (shrubby subformation)	80	160	2800	2800	2800	2800	2800

Table 3d Parameters that apply across all vegetation formations and land uses, including grid cell sizes relevant to resource utilisation (SC_CS) and dispersal (LC_CS) as well as minimum viable habitat area (MVH)

Entity name	SC_CS (m)	H min (%)	H max (%)	P min (m)	P max (m)	LC_CS (m)	MVH (ha)	DP min (m)	DP max (m)
Brown treecreeper	100	0	100	10	500	200	1000	10	3500

Table S4. Frequency table for sites according to (a) land use and (b) vegetation formation. Details of land use in Foster et al. (2017). D = GFS detected; ND = GFS not detected

(a) land use

	Land use 1		Land use 2		Land use 3		Land use 4		Land use 5		Land use 8		Land use 9		Site totals		
	Cleared		Crops without scattered trees		Crops with scattered trees		Perennial horticulture		Revegetation		State forest		State reserves				
	ND	D	ND	D	ND	D	ND	D	ND	D	ND	D	ND	D	ND	D	Total
Number of sites per land use	90	13	50	15	428	416	1	1	12	4	38	11	111	83	730	543	1273
Total number of sites per land use	103		65		844		2		16		49		194				
Proportion of sites (%)	8.1		5.1		66.3		0.2		1.3		3.8		15.2				100
land use area (ha)	99,028		2,102,038		2,584,016		10,078		46,058		40,638		197,547				5,079,403
Proportion of study region (5,079,403 ha) (%)	1.9		41.4		50.9		0.2		0.9		0.8		3.9				100
Ratio no. sites/land use area	1:961		1:32,339		1:3,061		1:5,039		1:2,878		1:829		1:1,018				

(b) vegetation formation

Vegetation formation (after Keith 2004)	Total records		Total number of sites	Proportion of sites for each vegetation formation (%)	Area of extant vegetation formation (ha) (37,620 ha were mapped as unknown)	Proportion of catchment (5,079,403 ha) (%)	Ratio no. sites/area of extant vegetation formation
	ND	D					
Rainforests	37	31	68	5.34	175,599	3.46	1:2,582
Wet sclerophyll forests (shrubby subformation)	0	0	0	0.00	345	0.01	0
Wet sclerophyll forests (grassy subformation)	0	0	0	0.00	40,893	0.81	0
Grassy woodlands	146	147	293	23.02	708,211	13.94	1:2,417
Grasslands	36	4	40	3.14	238,863	4.70	1:5,972
Dry sclerophyll forests (shrub/grass subformation)	113	39	152	11.94	555,488	10.94	1:3,655
Dry sclerophyll forests (shrubby subformation)	257	232	489	38.41	1,144,113	22.52	1:2,340
Heathlands	1	2	3	0.24	3685	0.07	1:1,228
Forested wetlands	0	1	1	0.08	18,104	0.36	1:18,104
Other wetlands	0	0	0	0.00	250	0.00	0
Semi-arid woodlands (grassy subformation)	130	85	215	16.9	1,969,177	38.8	1:9,159
Semi-arid woodlands (shrubby subformation)	10	2	12	0.94	88,027	1.73	1:7,336
total	730	543	1273	100.00	4,942,755	97.31	

Table S5. Modification of REMP models and results of discrimination analysis. Models sorted by increasing AUC value. Vegetation formations described in Appendix S2 Table S1. Land-use classes described in Foster et al. (2017). ↑ indicates values increased; ↓ indicates values decreased; –indicates no change

Model name	Generic focal species group		Model type	Variable evaluated against observational data		Behavioural parameter values			Behavioural models Direction and value of modification from base parameter values			Habitat suitability models Direction and value of modification from base expert-estimated parameter value for land-uses (land-use code)					Discrimination indices			
	GFS1	GFS2		REMP predicted occupancy	Habitat suitability	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Pastures and crops without scattered trees (2)	Pastures and crops with scattered trees (3)	State forests (8)	State reserves (9)	Modified vegetation formation (codes)	Sensitivity	Specificity	AUC	True Test Statistic
h_1GFS2M300_2		✓	habitat predictor		✓	1100	4800	500	–	–	–	–	↓20%	–	↓20%	4,6,7,12#	0.876	0.282	0.538	0.15788
h_1GFS2M200_2		✓	habitat predictor		✓	1100	4800	500	–	–	–	–	↓10%	–	↓10%	4,6,7,12#	0.876	0.282	0.541	0.15788
h_1GFS1M200_2	✓		habitat predictor		✓	1100	3300	400	–	–	–	–	↓10%	–	↓10%	4,6,7,12#	0.585	0.467	0.542	0.05213
h_1GFS2M200_1		✓	habitat predictor		✓	1100	4800	500	–	–	–	–	↓10%	–	↓10%	4,6,7,12,13^	0.876	0.282	0.542	0.15788
h_1GFS2M300_1		✓	habitat predictor		✓	1100	4800	500	–	–	–	–	↓20%	–	↓20%	4,6,7,12,13^	0.876	0.282	0.542	0.15788
h_1GFS1M200_1	✓		habitat predictor		✓	1100	3300	400	–	–	–	–	↓10%	–	↓10%	4,6,7,12,13^	0.581	0.479	0.543	0.06080
h_1GFS2M101_1		✓	habitat predictor		✓	1100	4800	500	–	–	–	↓10%	↓10%	↓10%	↓10%	4,6,12*	0.876	0.282	0.544	0.15788
h_1GFS1CU	✓		habitat predictor		✓	1100	3300	400	–	–	–	–	–	–	–		0.876	0.282	0.544	0.15788
h_1GFS2M102_1		✓	habitat predictor		✓	1100	4800	500	–	–	–	↓20%	↓20%	↓20%	↓20%	4,6,12*	0.876	0.282	0.553	0.15788
h_1GFS1M100	✓		habitat predictor		✓	1100	3300	400	–	–	–	↑5%	↑5%	↓5%	↓5%	4,6,12*	0.876	0.282	0.554	0.15788
h_1GFS2M103_1		✓	habitat predictor		✓	1100	4800	500	–	–	–	↓20%	↓20%	↓30%	↓30%	4,6,12*	0.876	0.282	0.555	0.15788
h_1GFS2CU		✓	habitat predictor		✓	1100	4800	500	–	–	–	–	–	–	–		0.876	0.282	0.555	0.15788
h_1GFS2M201		✓	habitat predictor		✓	1100	4800	500	–	–	–	↓10%	↓10%	↓10%	↓10%	all vegetation formations/land-use combinations reduced 10%	0.876	0.282	0.555	0.15788
h_1GFS2M301		✓	habitat predictor		✓	1100	4800	500	–	–	–	↓20%	↓20%	↓20%	↓20%	all vegetation formations/land-use combinations reduced 20%	0.876	0.282	0.555	0.15788
h_1GFS2M100		✓	habitat predictor		✓	1100	4800	500	–	–	–	↑5%	↑5%	↓5%	↓5%	4,6,12*	0.876	0.282	0.556	0.15788
h_1GFS2M101_2		✓	habitat predictor		✓	1100	4800	500	–	–	–	↑10%	↑10%	↓10%	↓10%	4,6,12*	0.876	0.282	0.561	0.15788
h_1GFS2M102_2		✓	habitat predictor		✓	1100	4800	500	–	–	–	↑20%	↑20%	↓20%	↓20%	4,6,12*	0.876	0.282	0.578	0.15788
h_1GFS2M103_2		✓	habitat predictor		✓	1100	4800	500	–	–	–	↑20%	↑20%	↓30%	↓30%	4,6,12*	0.876	0.282	0.579	0.15788
GFS1M24	✓		behavioural	✓		1320	3960	400	↑20%	↑20%	–	–	–	–	–		0.572	0.558	0.582	0.12975
GFS1M21	✓		behavioural	✓		1320	3960	320	↑20%	↑20%	↓20%	–	–	–	–		0.548	0.579	0.583	0.12790
GFS1M200	✓		habitat suitability	✓		1100	3300	400	–	–	–	–	↓10%	–	↓10%	4,6,7,12,13^	0.481	0.644	0.583	0.12464
GFS1M200_2	✓		habitat suitability	✓		1100	3300	400	–	–	–	–	↓10%	–	↓10%	4,6,7,12#	0.481	0.644	0.583	0.12464
GFS1M12	✓		behavioural	✓		1100	3960	320	–	↑20%	↓20%	–	–	–	–		0.534	0.584	0.583	0.11738

Model name	Generic focal species group		Model type	Variable evaluated against observational data		Behavioural parameter values			Behavioural models: Direction and value of modification from base parameter values			Habitat suitability models: Direction and value of modification from base expert-estimated parameter value for land-uses (land-use code)					Discrimination indices			
	GFS1	GFS2		REMP predicted occupancy	Habitat suitability	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Pastures and crops without scattered trees (2)	Pastures and crops with scattered trees (3)	State forests (8)	State reserves (9)	Modified vegetation formation (codes)	Sensitivity	Specificity	AUC	True Test Statistic
GFS1M15	✓		behavioural	✓		1100	3960	400	–	↑20%	–	–	–	–	–		0.572	0.556	0.583	0.12838
GFS1M20	✓		behavioural	✓		1320	3300	320	↑20%	–	↓20%	–	–	–	–		0.494	0.634	0.583	0.12785
GFS1M1	✓		behavioural	✓		880	2640	320	↓20%	↓20%	↓20%	–	–	–	–		0.484	0.630	0.583	0.11460
GFS1M18	✓		behavioural	✓		1100	3960	480	–	↑20%	↑20%	–	–	–	–		0.623	0.540	0.583	0.16313
GFS2M51		✓	behavioural	✓		550	2400	250	↓50%	↓50%	↓50%	–	–	–	–		0.611	0.555	0.583	0.16540
GFS1M3	✓		behavioural	✓		880	3960	320	↓20%	↑20%	↓20%	–	–	–	–		0.634	0.537	0.583	0.17136
GFS1M8	✓		behavioural	✓		880	3300	480	↓20%	–	↑20%	–	–	–	–		0.636	0.529	0.584	0.16496
GFS1M2	✓		behavioural	✓		880	3300	320	↓20%	–	↓20%	–	–	–	–		0.556	0.568	0.584	0.12425
GFS1M5	✓		behavioural	✓		880	3300	400	↓20%	–	–	–	–	–	–		0.614	0.545	0.584	0.15947
GFS1M27	✓		behavioural	✓		1320	3960	480	↑20%	↑20%	↑20%	–	–	–	–		0.623	0.542	0.584	0.16587
GFS1M11	✓		behavioural	✓		1100	3300	320	–	–	↓20%	–	–	–	–		0.484	0.637	0.584	0.12145
GFS1CU	✓		behavioural	✓		1100	3300	400	–	–	–	–	–	–	–		0.517	0.611	0.584	0.12833
GFS1M23	✓		behavioural	✓		1320	3300	400	↑20%	–	–	–	–	–	–		0.517	0.611	0.584	0.12833
GFS1M19	✓		behavioural	✓		1320	2640	320	↑20%	↓20%	↓20%	–	–	–	–		0.356	0.668	0.584	0.02498
GFS1M4	✓		behavioural	✓		880	2640	400	↓20%	↓20%	–	–	–	–	–		0.517	0.603	0.585	0.12011
GFS1M10	✓		behavioural	✓		1100	2640	320	–	↓20%	↓20%	–	–	–	–		0.355	0.681	0.585	0.03548
GFS1M26	✓		behavioural	✓		1320	3300	480	↑20%	–	↑20%	–	–	–	–		0.548	0.575	0.585	0.12379
GFS1M17	✓		behavioural	✓		1100	3300	480	–	–	↑20%	–	–	–	–		0.550	0.575	0.585	0.12562
GFS1M16	✓		behavioural	✓		1100	2640	480	–	↓20%	↑20%	–	–	–	–		0.484	0.632	0.585	0.11597
GFS1M7	✓		behavioural	✓		880	2640	480	↓20%	↓20%	↑20%	–	–	–	–		0.559	0.560	0.585	0.11969
GFS1M100	✓		habitat suitability	✓		1100	3300	400	–	–	–	↑5%	↑5%	↓5%	↓5%	4,6,12*	0.525	0.600	0.585	0.12468
GFS1M22	✓		behavioural	✓		1320	2640	400	↑20%	↓20%	–	–	–	–	–		0.472	0.649	0.585	0.12098
GFS2M10	✓		behavioural	✓		1100	3840	400	–	↓20%	↓20%	–	–	–	–		0.638	0.537	0.586	0.17501
GFS1M25	✓		behavioural	✓		1320	2640	480	↑20%	↓20%	↑20%	–	–	–	–		0.483	0.632	0.586	0.11414
GFS1M13	✓		behavioural	✓		1100	2640	400	–	↓20%	–	–	–	–	–		0.472	0.652	0.586	0.12372
GFS2M46		✓	behavioural	✓		770	2880	500	↓30%	↓40%	–	–	–	–	–		0.645	0.522	0.586	0.16726
GFS2M40		✓	behavioural	✓		660	2880	500	↓40%	↓40%	–	–	–	–	–		0.702	0.482	0.587	0.18420
GFS2M54		✓	behavioural	✓		550	2400	500	↓50%	↓50%	–	–	–	–	–		0.667	0.488	0.587	0.15495
GFS2M22		✓	behavioural	✓		1320	3840	500	↑20%	↓20%	–	–	–	–	–		0.638	0.541	0.587	0.17912
GFS2M19		✓	behavioural	✓		1320	3840	400	↑20%	↓20%	↓20%	–	–	–	–		0.612	0.552	0.587	0.16449
GFS1M9	✓		behavioural	✓		880	3960	480	↓20%	↑20%	↑20%	–	–	–	–		0.654	0.514	0.588	0.16818
GFS2M63		✓	behavioural	✓		1320	2880	500	↑20%	↓40%	–	–	–	–	–		0.541	0.595	0.588	0.13565
GFS1M6	✓		behavioural	✓		880	3960	400	↓20%	↑20%	–	–	–	–	–		0.640	0.523	0.589	0.16314
GFS2M50		✓	behavioural	✓		660	4800	500	↓40%	–	–	–	–	–	–		0.766	0.419	0.590	0.18517
GFS2M300		✓	habitat suitability	✓		1100	4800	500	–	–	–	–	↓20%	–	↓20%	4,6,7,12,13^	0.667	0.529	0.591	0.19604
GFS2M21		✓	behavioural	✓		1320	5760	400	↑20%	↑20%	↓20%	–	–	–	–		0.706	0.488	0.591	0.19334

Model name	Generic focal species group		Model type	Variable evaluated against observational data		Behavioural parameter values			Behavioural models: Direction and value of modification from base parameter values			Habitat suitability models: Direction and value of modification from base expert-estimated parameter value for land-uses (land-use code)					Discrimination indices			
	GFS1	GFS2		REMP predicted occupancy	Habitat suitability	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Pastures and crops without scattered trees (2)	Pastures and crops with scattered trees (3)	State forests (8)	State reserves (9)	Modified vegetation formation (codes)	Sensitivity	Specificity	AUC	True Test Statistic
GFS2M300_2		✓	habitat suitability	✓		1100	3300	400	–	–	–	–	↓20%	–	↓20%	4,6,7,12#	0.667	0.529	0.591	0.19604
GFS2M20		✓	behavioural	✓		1320	4800	400	↑20%	–	↓20%	–	–	–	–		0.667	0.532	0.591	0.19878
GFS2M11		✓	behavioural	✓		1320	5760	500	↑20%	↑20%	–	–	–	–	–		0.702	0.497	0.591	0.19927
GFS2M15		✓	behavioural	✓		1100	5760	500	–	↑20%	–	–	–	–	–		0.726	0.449	0.592	0.17509
GFS2M34		✓	behavioural	✓		770	3360	650	↓30%	↓30%	↑30%	–	–	–	–		0.724	0.459	0.592	0.18285
GFS2M23		✓	behavioural	✓		1320	4800	500	↑20%	–	–	–	–	–	–		0.691	0.507	0.592	0.19789
GFS2M47		✓	behavioural	✓		1430	4800	500	↑30%	–	–	–	–	–	–		0.680	0.526	0.592	0.20610
GFS2M49		✓	behavioural	✓		770	4800	500	↓30%	–	–	–	–	–	–		0.733	0.447	0.592	0.17966
GFS2M104		✓	behavioural/habitat suitability	✓		1320	3840	500	↑20%	↓20%	–	↓20%	↓20%	↓30%	↓30%	4,6,12*	0.592	0.567	0.592	0.15945
GFS2M1		✓	behavioural	✓		880	3840	400	↓20%	↓20%	↓20%	–	–	–	–		0.695	0.507	0.593	0.20155
GFS2M33		✓	behavioural	✓		770	6240	500	↓30%	↑30%	–	–	–	–	–		0.768	0.401	0.593	0.16919
GFS2M13		✓	behavioural	✓		1100	3840	500	–	↓20%	–	–	–	–	–		0.647	0.525	0.593	0.17182
GFS2CU		✓	behavioural	✓		1100	4800	500	–	–	–	–	–	–	–		0.707	0.477	0.593	0.18421
GFS2M25		✓	behavioural	✓		1320	3840	600	↑20%	↓20%	↑20%	–	–	–	–		0.640	0.530	0.593	0.16999
GFS2M48		✓	behavioural	✓		1540	4800	500	↑40%	–	–	–	–	–	–		0.664	0.534	0.593	0.19787
GFS2M31		✓	behavioural	✓		770	3360	500	↓30%	↓30%	–	–	–	–	–		0.698	0.493	0.593	0.19151
GFS2M301		✓	habitat suitability	✓		1100	4800	500	–	–	–	↓20%	↓20%	↓20%	↓20%	all vegetation formations/land-use combinations reduced 20%	0.664	0.532	0.593	0.19513
GFS2M43		✓	behavioural	✓		660	2880	800	↓40%	↓40%	↑40%	–	–	–	–		0.733	0.440	0.593	0.17282
GFS2M12		✓	behavioural	✓		1100	5760	400	–	↑20%	↓20%	–	–	–	–		0.718	0.464	0.593	0.18285
GFS2M2		✓	behavioural	✓		880	4800	400	↓20%	–	↓20%	–	–	–	–		0.720	0.460	0.593	0.18057
GFS2M9		✓	behavioural	✓		880	5760	600	↓20%	↑20%	↑20%	–	–	–	–		0.768	0.414	0.593	0.18152
GFS2M200_2		✓	habitat suitability	✓		1100	3300	400	–	–	–	–	↓10%	–	↓10%	4,6,7,12#	0.697	0.493	0.594	0.18968
GFS2M200		✓	habitat suitability	✓		1100	4800	500	–	–	–	–	↓10%	–	↓10%	4,6,7,12,13^	0.697	0.493	0.594	0.18968
GFS2M5		✓	behavioural	✓		880	4800	500	↓20%	–	–	–	–	–	–		0.731	0.448	0.594	0.17921
GFS2M100		✓	habitat suitability	✓		1100	4800	500	–	–	–	↑5%	↑5%	↓5%	↓5%	4,6,12*	0.713	0.475	0.594	0.18832
GFS2M55			behavioural	✓		550	4800	500	↓50%	–	–	–	–	–	–		0.770	0.401	0.594	0.17102
GFS2M201		✓	habitat suitability	✓		1100	4800	500	–	–	–	↓10%	↓10%	↓10%	↓10%	all vegetation formations/land-use combinations reduced 10%	0.697	0.497	0.594	0.19379

Model name	Generic focal species group		Model type	Variable evaluated against observational data		Behavioural parameter values			Behavioural models: Direction and value of modification from base parameter values			Habitat suitability models: Direction and value of modification from base expert-estimated parameter value for land-uses (land-use code)					Discrimination indices			
	GFS1	GFS2		REMP predicted occupancy	Habitat suitability	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Pastures and crops without scattered trees (2)	Pastures and crops with scattered trees (3)	State forests (8)	State reserves (9)	Modified vegetation formation (codes)	Sensitivity	Specificity	AUC	True Test Statistic
GFS2M3		✓	behavioural	✓		880	5760	400	↓20%	↑20%	↓20%	–	–	–	–		0.737	0.447	0.594	0.18332
GFS2M18		✓	behavioural	✓		1100	5760	600	–	↑20%	↑20%	–	–	–	–		0.757	0.447	0.594	0.20343
GFS2M27		✓	behavioural	✓		1320	5760	600	↑20%	↑20%	↑20%	–	–	–	–		0.724	0.453	0.594	0.17737
GFS2M56		✓	behavioural	✓		550	7200	500	↓50%	↑50%	–	–	–	–	–		0.784	0.370	0.595	0.15414
GFS2M59		✓	behavioural	✓		550	7200	750	↓50%	↑50%	↑50%	–	–	–	–		0.832	0.325	0.595	0.15647
GFS2M17		✓	behavioural	✓		1100	4800	600	–	–	↑20%	–	–	–	–		0.724	0.458	0.595	0.18148
GFS2M24		✓	behavioural	✓		1320	5760	500	↑20%	↑20%	–	–	–	–	–		0.709	0.478	0.595	0.18741
GFS2M16		✓	behavioural	✓		1100	3840	600	–	↓20%	↑20%	–	–	–	–		0.691	0.501	0.595	0.19241
GFS2M102		✓	habitat suitability	✓		1100	3300	400	–	–	–	↓20%	↓20%	↓20%	↓20%	4,6,12*	0.686	0.504	0.595	0.18967
GFS2M101		✓	habitat suitability	✓		1100	3300	400	–	–	–	↓10%	↓10%	↓10%	↓10%	4,6,12*	0.702	0.485	0.595	0.18694
GFS2M8		✓	behavioural	✓		880	4800	600	↓20%	–	↑20%	–	–	–	–		0.761	0.441	0.596	0.20161
GFS2M7		✓	behavioural	✓		880	3840	600	↓20%	↓20%	↑20%	–	–	–	–		0.726	0.458	0.596	0.18331
GFS2M4		✓	behavioural	✓		880	3840	500	↓20%	↓20%	–	–	–	–	–		0.713	0.475	0.596	0.18832
GFS2M103		✓	habitat suitability	✓		1100	3300	400	–	–	–	↓20%	↓20%	↓30%	↓30%	4,6,12*	0.684	0.507	0.596	0.19058
GFS2M101_2		✓	habitat suitability	✓		1100	3300	400	–	–	–	↑10%	↑10%	↓10%	↓10%	4,6,12*	0.715	0.467	0.597	0.18193
GFS2M26		✓	behavioural	✓		1320	4800	600	↑20%	–	↑20%	–	–	–	–		0.707	0.486	0.597	0.19380
GFS2M6		✓	behavioural	✓		880	5760	500	↓20%	↑20%	–	–	–	–	–		0.762	0.432	0.597	0.19385
GFS2M400	✓		habitat suitability	✓		1100	3300	400	–	–	–	–	↓ according to observations	–	↓ according to observations	4,6,7,12#	0.642	0.566	0.597	0.20744
GFS2M41		✓	behavioural	✓		660	4800	500	↓40%	–	–	–	–	–	–		0.740	0.419	0.597	0.15958
GFS2M42		✓	behavioural	✓		660	6720	500	↓40%	↑40%	–	–	–	–	–		0.770	0.385	0.598	0.15458
GFS2M102_2		✓	habitat suitability	✓		1100	3300	400	–	–	–	↑20%	↑20%	↓20%	↓20%	4,6,12*	0.724	0.462	0.598	0.18559
GFS2M90		✓	behavioural	✓		1100	7200	500	–	↑50%	–	–	–	–	–		0.735	0.436	0.599	0.17053
GFS2M103_2		✓	habitat suitability	✓		1100	3300	400	–	–	–	↑20%	↑20%	↓30%	↓30%	4,6,12*	0.722	0.462	0.599	0.18376
GFS2M32		✓	behavioural	✓		770	4800	500	↓30%	–	–	–	–	–	–		0.729	0.447	0.600	0.17601
GFS1M400	✓		habitat suitability	✓		1100	3300	400	–	–	–	–	↓ according to observations	–	↓ according to observations	4,6,7,12#	0.342	0.697	0.601	0.03912
GFS2M92		✓	behavioural	✓		1100	4800	750	–	–	↑50%	–	–	–	–		0.726	0.449	0.601	0.17509
GFS2M245		✓	behavioural/habitat suitability	✓		660	6720	500	↓40%	↑40%	↑40%	–	↓10%	–	↓10%	4,6,7,12,13^	0.784	0.371	0.602	0.15551
GFS245		✓	behavioural	✓		660	6720	500	↓40%	↑40%	↑40%	–	–	–	–		0.817	0.362	0.602	0.17883
GFS2M72		✓	behavioural	✓		1100	6240	500	–	↑30%	–	–	–	–	–		0.731	0.448	0.603	0.17921
GFS2M81		✓	behavioural	✓		1100	6720	500	–	↑40%	–	–	–	–	–		0.733	0.442	0.604	0.17556
GFS2M74		✓	behavioural	✓		1100	4800	650	–	–	↑30%	–	–	–	–		0.726	0.455	0.605	0.18057

Model name	Generic focal species group		Model type	Variable evaluated against observational data		Behavioural parameter values			Behavioural models: Direction and value of modification from base parameter values			Habitat suitability models: Direction and value of modification from base expert-estimated parameter value for land-uses (land-use code)					Discrimination indices			
	GFS1	GFS2		REMP predicted occupancy	Habitat suitability	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Minimum viable habitat (MVH) (ha)	Dispersal (DP)(m)	Forage (P)(m)	Pastures and crops without scattered trees (2)	Pastures and crops with scattered trees (3)	State forests (8)	State reserves (9)	Modified vegetation formation (codes)	Sensitivity	Specificity	AUC	True Test Statistic
GFS2M83		✓	behavioural	✓		1100	4800	700	–	–	↑40%	–	–	–	–		0.726	0.460	0.607	0.18605
h_1GFS2M400		✓	habitat predictor		✓	1100	4800	500	–	–	–	–	↓ according to observations	–	↓ according to observations	4,6,7,12#	0.558	0.644	0.631	0.20142
h_1GFS1M400		✓	habitat predictor		✓	1100	3300	400	–	–	–	–	↓ according to observations	–	↓ according to observations	4,6,7,12#	0.558	0.644	0.633	0.20142

*rated most suitable (100%) formations and sub-formations; ^ most extensive formations; # most sampled formations and sub-formations.

Reference

Doerr V, Williams K, Drielsma M et al (2013) Designing landscapes for biodiversity under climate change, Final Report. National Climate Change Adaptation Research Facility, Gold Coast, Queensland

Foster E, Love, J. Rader et al. (2017) A revegetation strategy using a fragmentation-sensitive generic focal species metapopulation model. To be submitted

Keith, DA (2004) Ocean shores to desert dunes: the native vegetation of New South Wales and the ACT. Department of Environment and Conservation (NSW), Hurstville, NSW

Fig. S1. Habitat suitability (left) and predicted metapopulation occupancy and detection/non-detection sites (right) for (a) GFS1 and (b) GFS2. White areas indicate no value for the attribute.

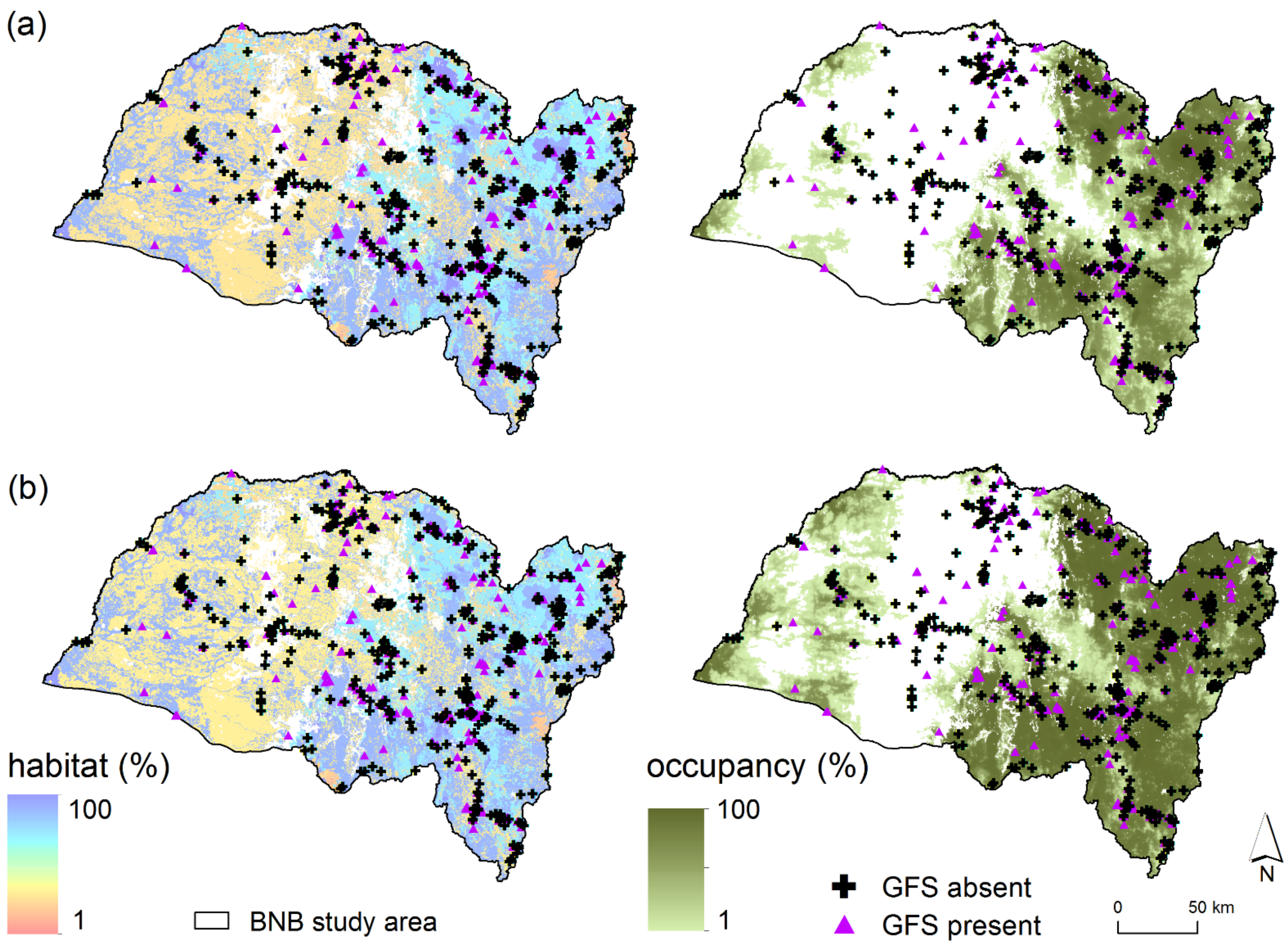
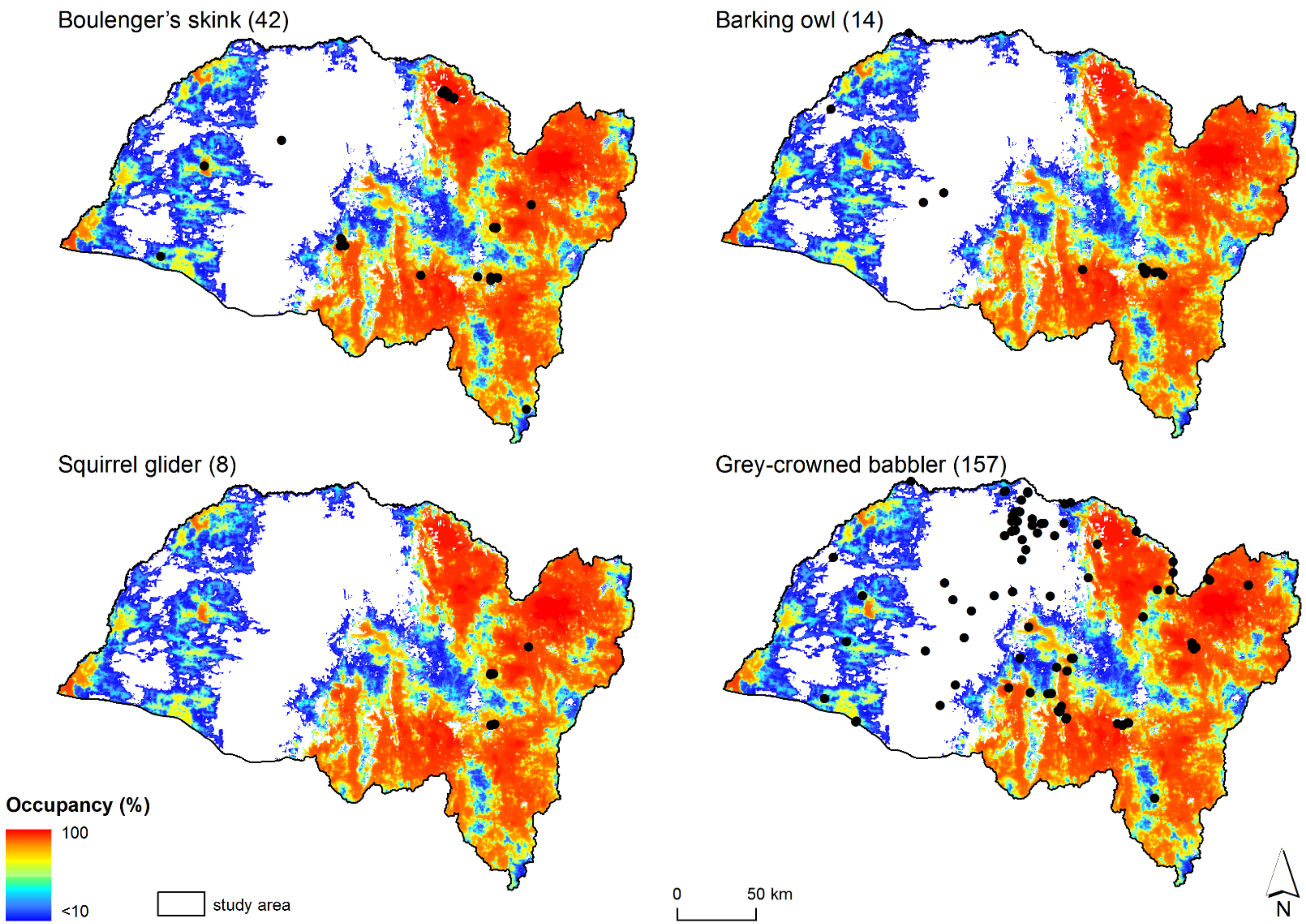


Fig. S2. Individual records of constituent species of the GFS across predicted metapopulation occupancy for GFS2 (base parameter values). White portions of study area indicate no populations are predicted to occur. Numbers in parentheses correspond to number of detection records.



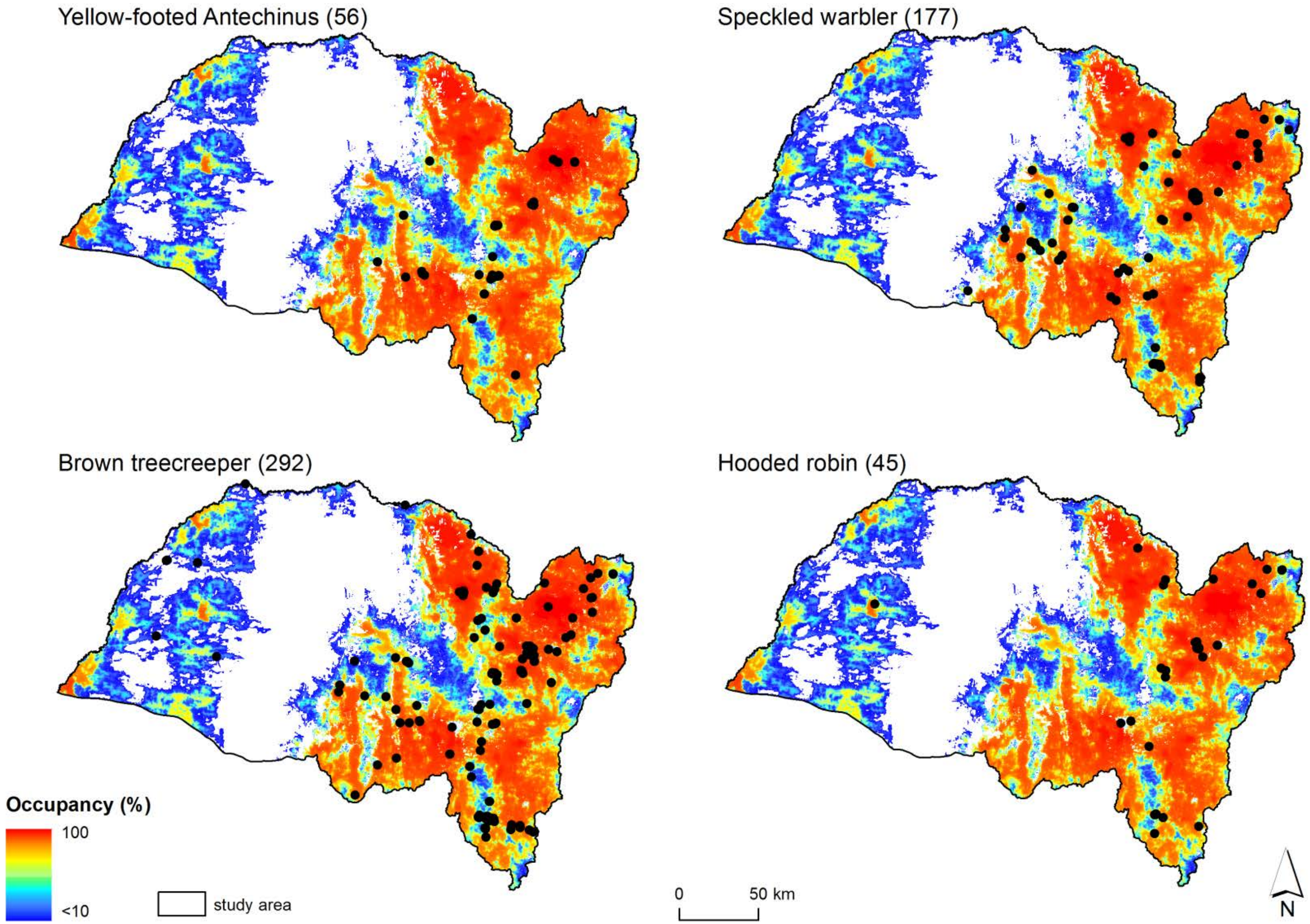

Yellow-footed Antechinus (56)
Speckled warbler (177)
Brown treecreeper (292)
Hooded robin (45)
Occupancy (%)
100
<10
study area
0
50 km
N

Fig. S3. Predicted metapopulation occupancy maps for GFS2 (base parameter values) and brown treecreeper. White portion of study area indicate no populations are predicted to occur. Predicted brown treecreeper occupancy extends almost entirely (99.1%) within the predicted occupancy of the GFS2. The difference map illustrates the absolute difference in probabilities values between GFS2 and brown treecreeper (yellow indicates no change).

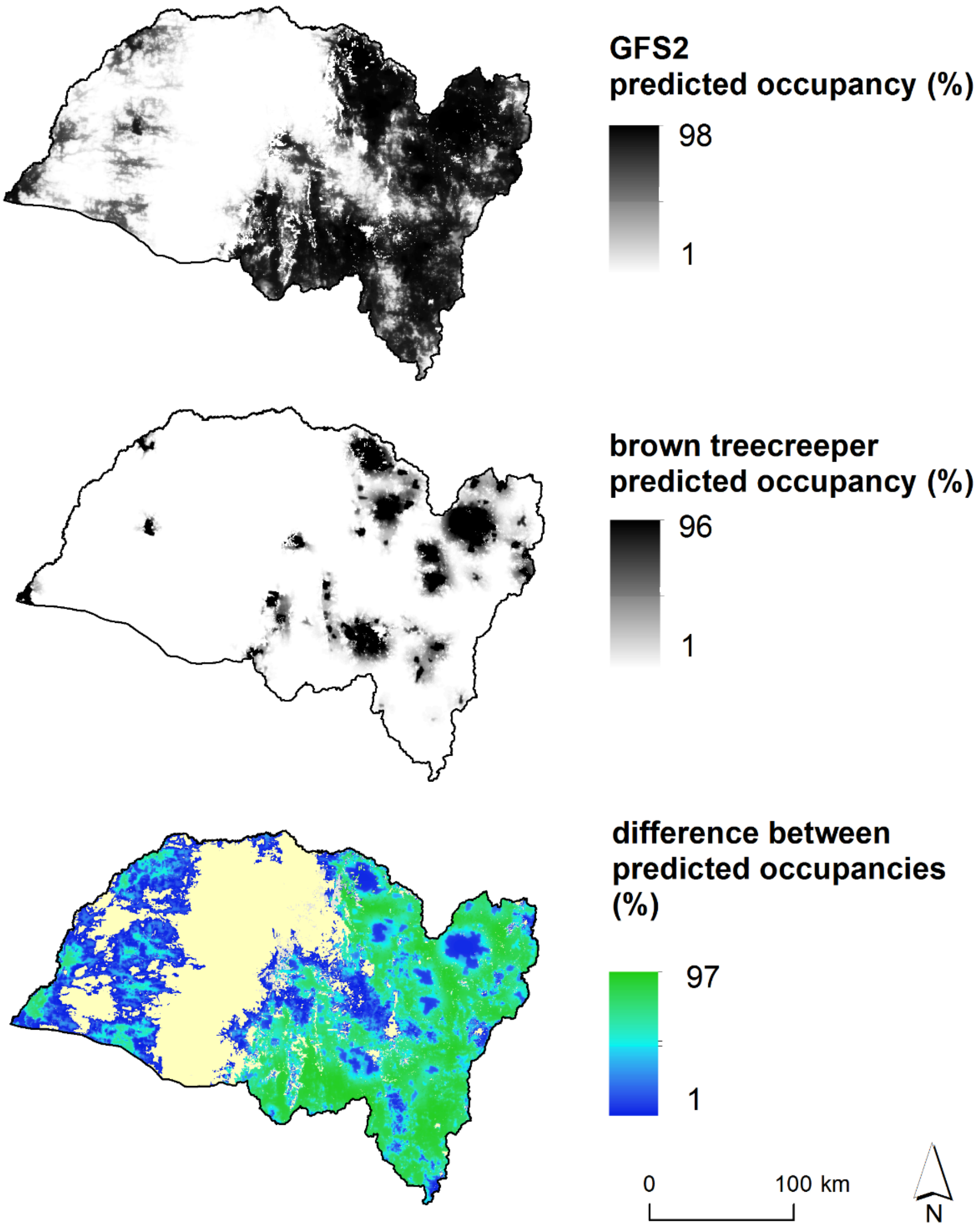
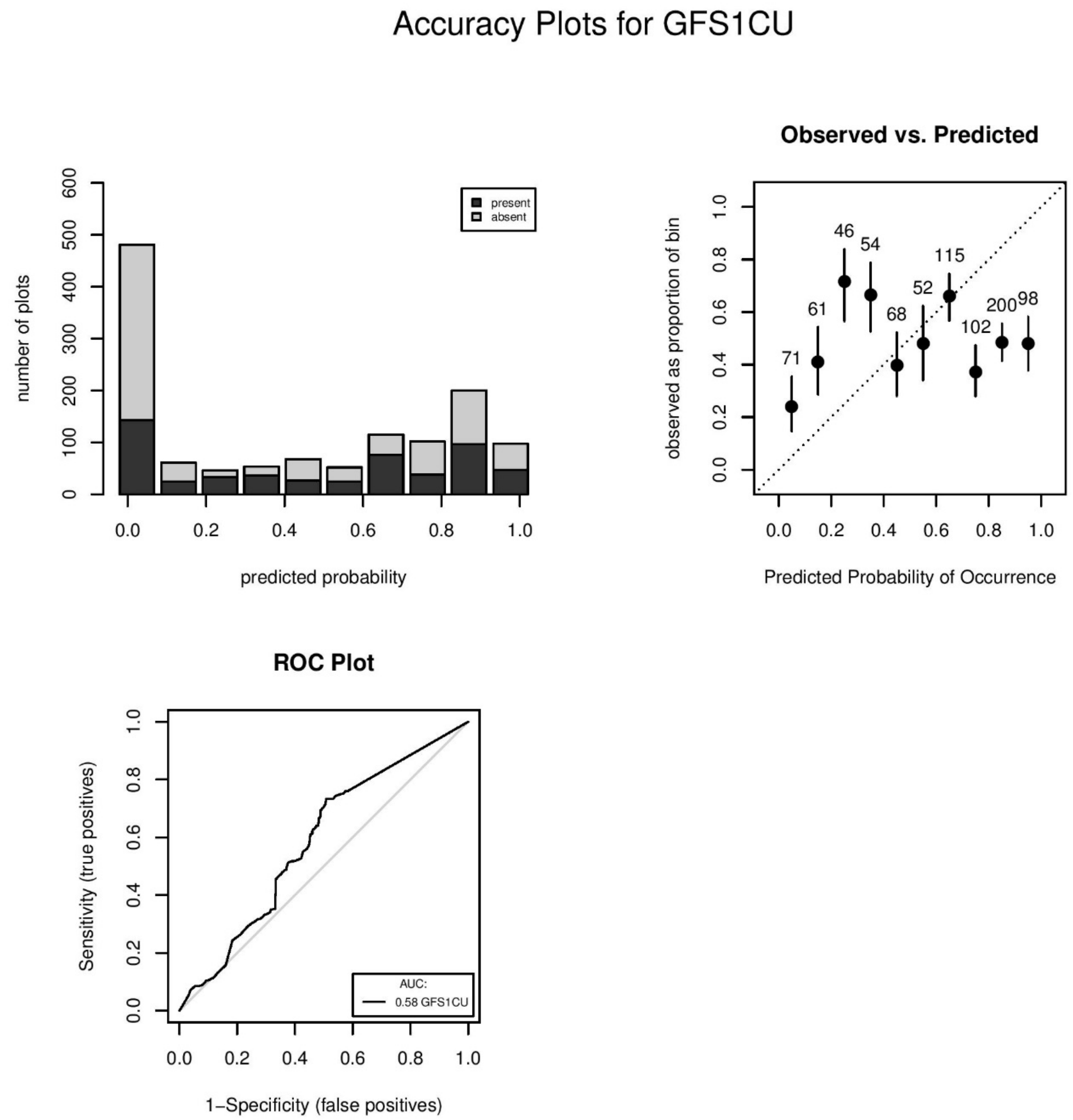
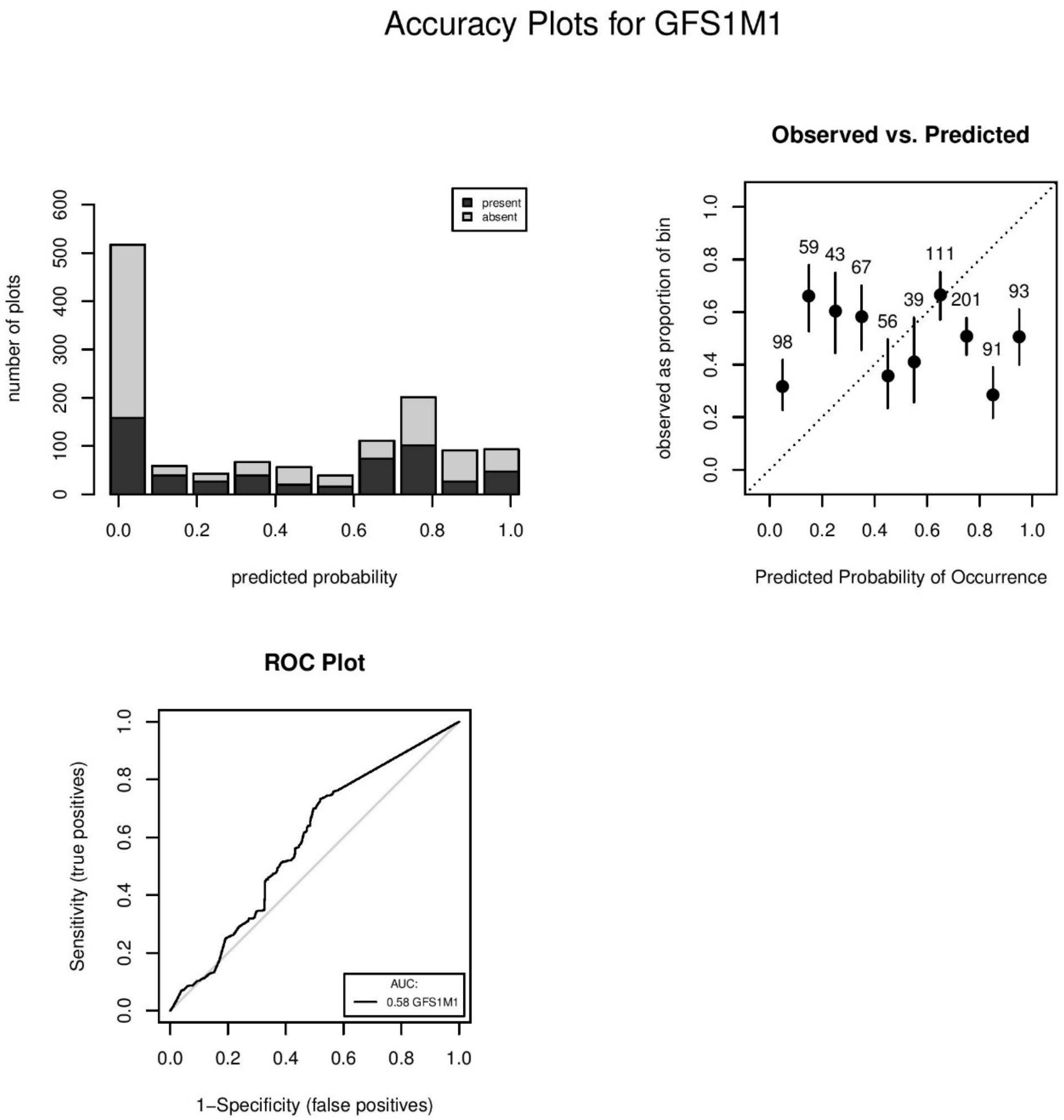
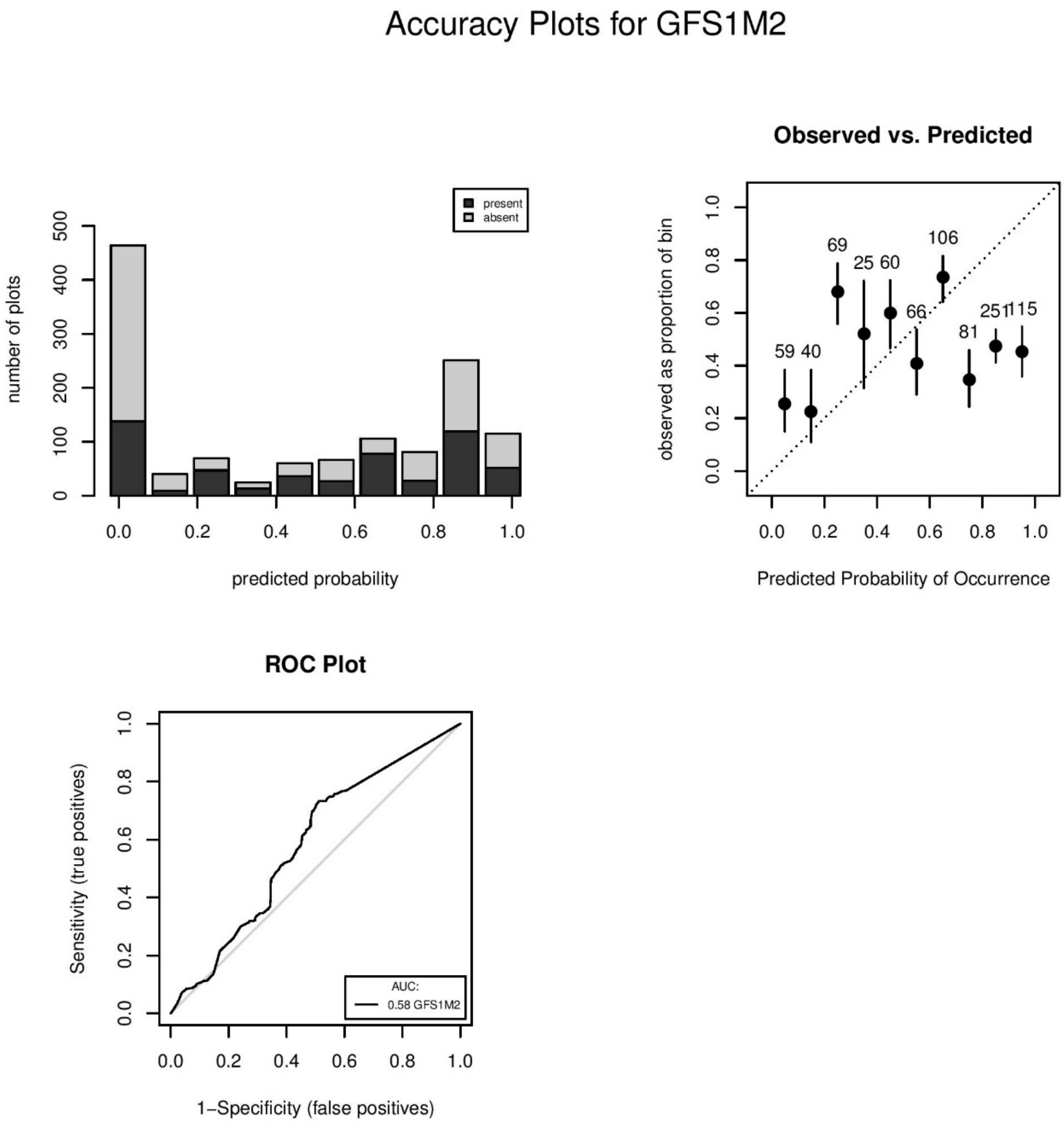
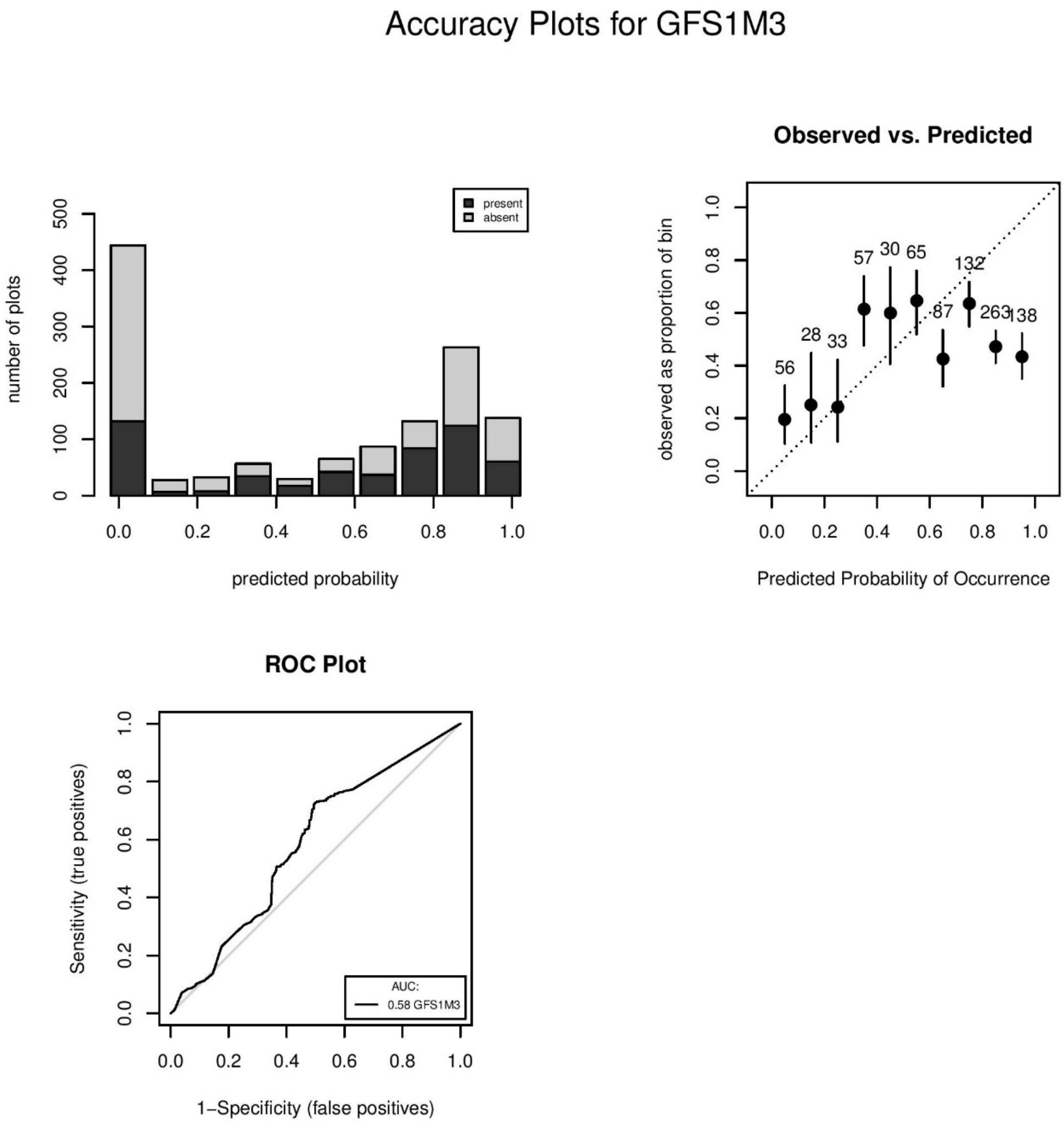


Fig. S4. Accuracy plots for predictive models (120 models), displaying discrimination and calibration. Discrimination is depicted in first two plots: distribution of observed occupied (present) and unoccupied (absent) sites as a function of predicted probability (top left), and the receiver operating curve (ROC) depicting the relationship between false positives and true positives, along with the area under the curve (AUC) value (bottom left). Calibration, the relationship between predicted probability of occurrence and the proportion of sites observed to be occupied (number of sites in each bin and the 95% confidence limits are shown), displays goodness-of-fit (top right). Model description are listed in Table S5. GFS1 = i.e. 25th percentile values for movement distances and the 25th percentile values for minimum viable habitat area for the group; GFS2 = median values for movement distances and the 25th percentile values for minimum viable habitat area for the group

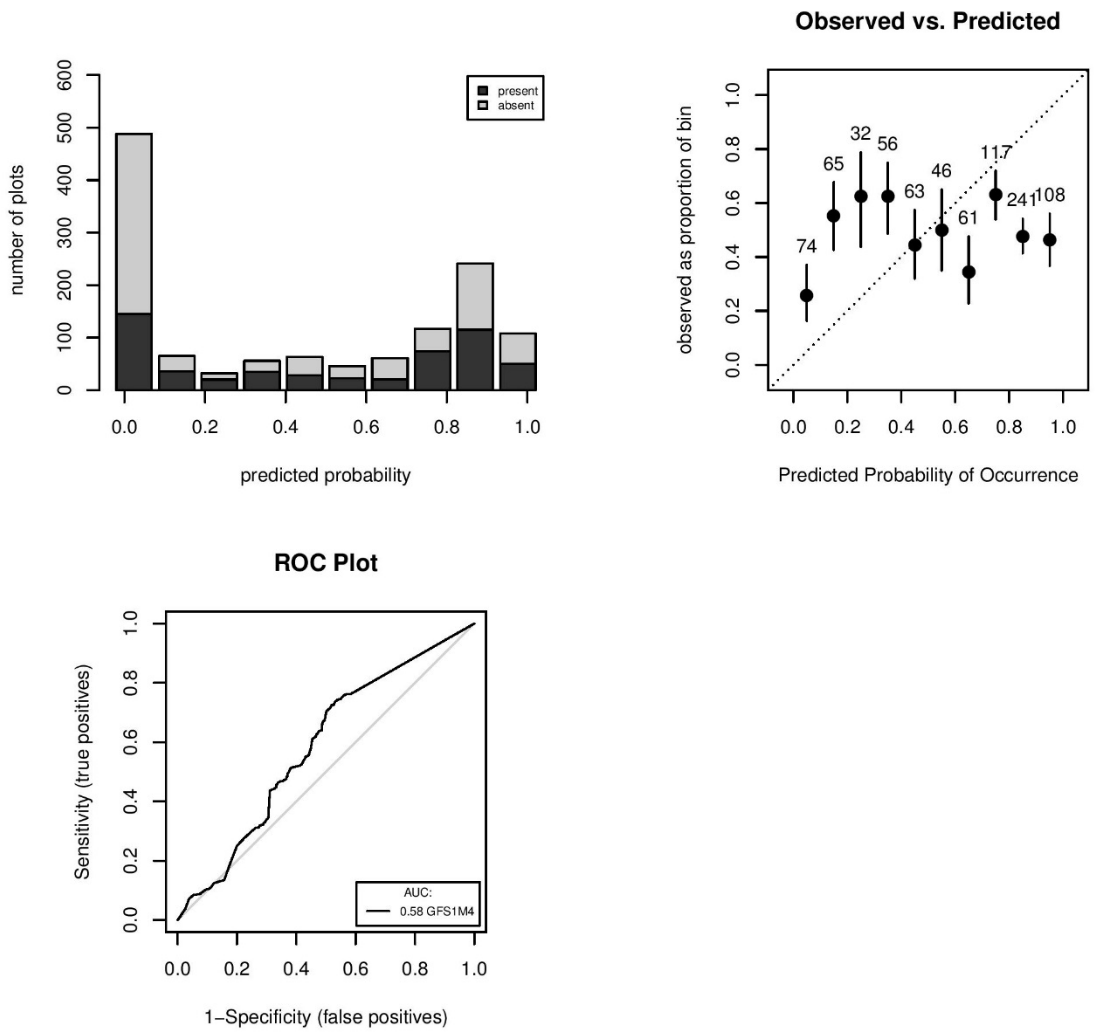

Accuracy Plots for GFS1CU
number of plots
0
100
200
300
400
500
600
present
absent
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
71
61
46
54
68
52
115
102
200
98
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.58 GFS1CU
1−Specificity (false positives)

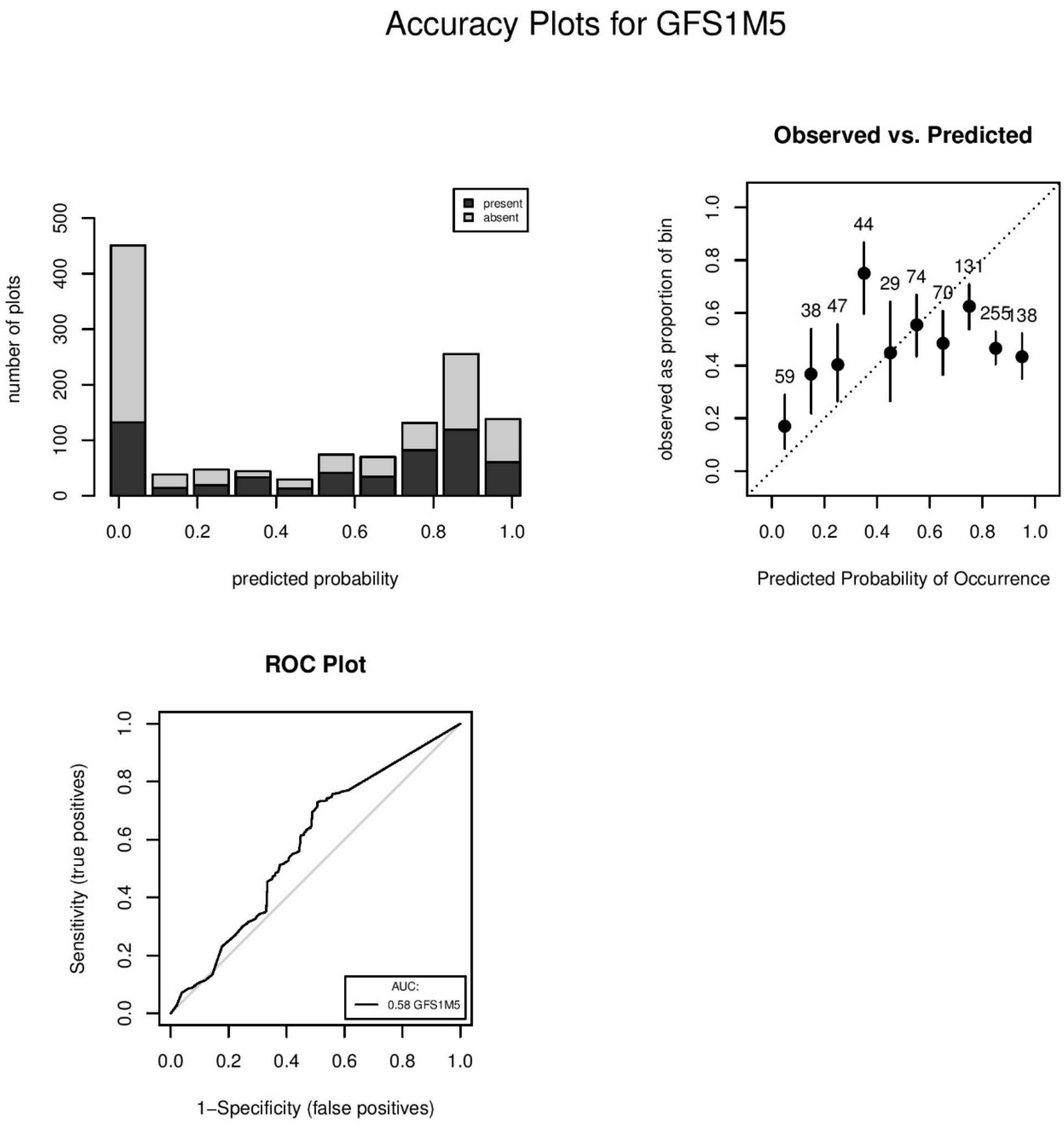

Accuracy Plots for GFS1M1
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
98
59
43
67
56
39
111
201
91
93
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M1


Accuracy Plots for GFS1M2
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
59 40
69
25 60
66
106
81
251115
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M2

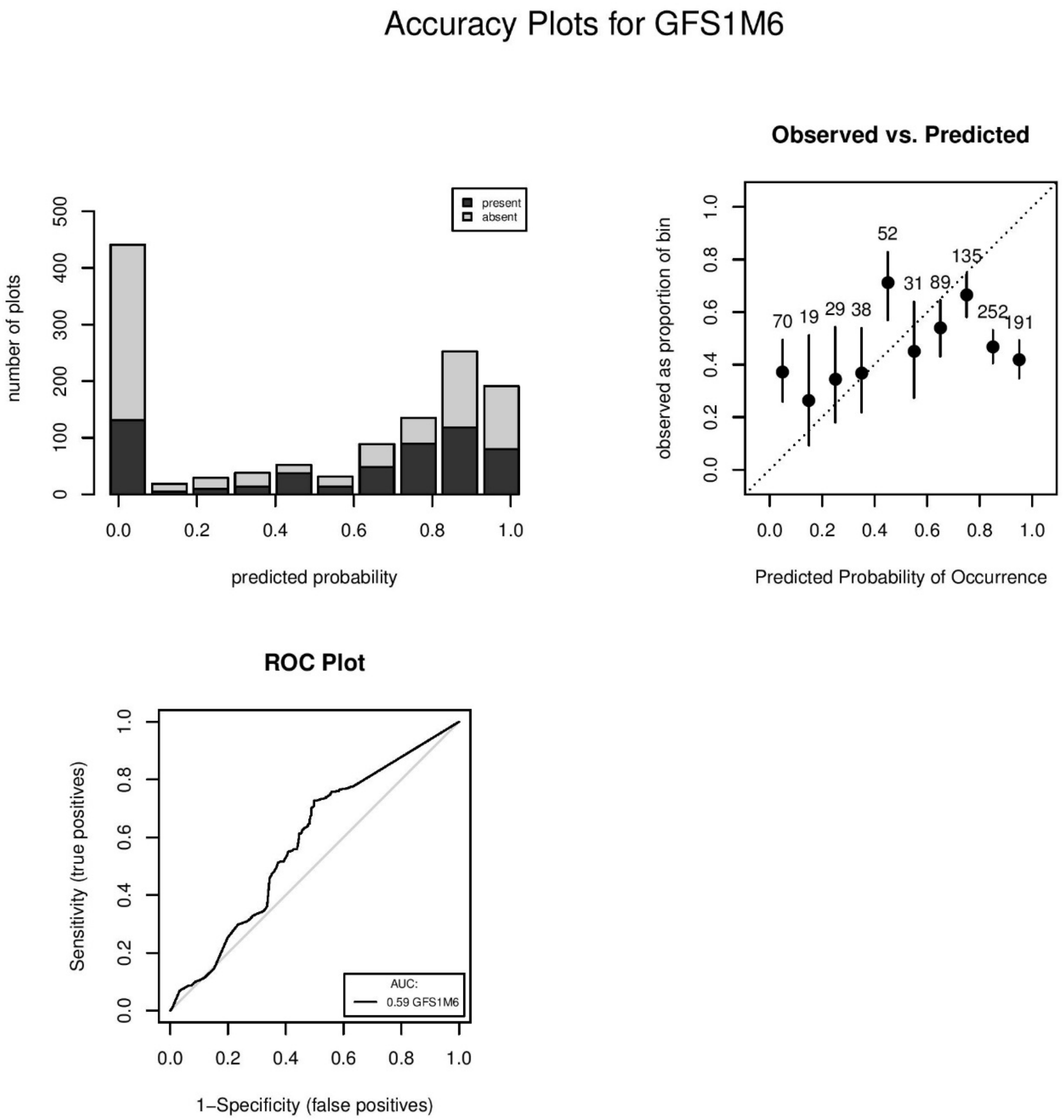

Accuracy Plots for GFS1M3
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
56
28
33
57
30
65
87
132
263
138
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M3

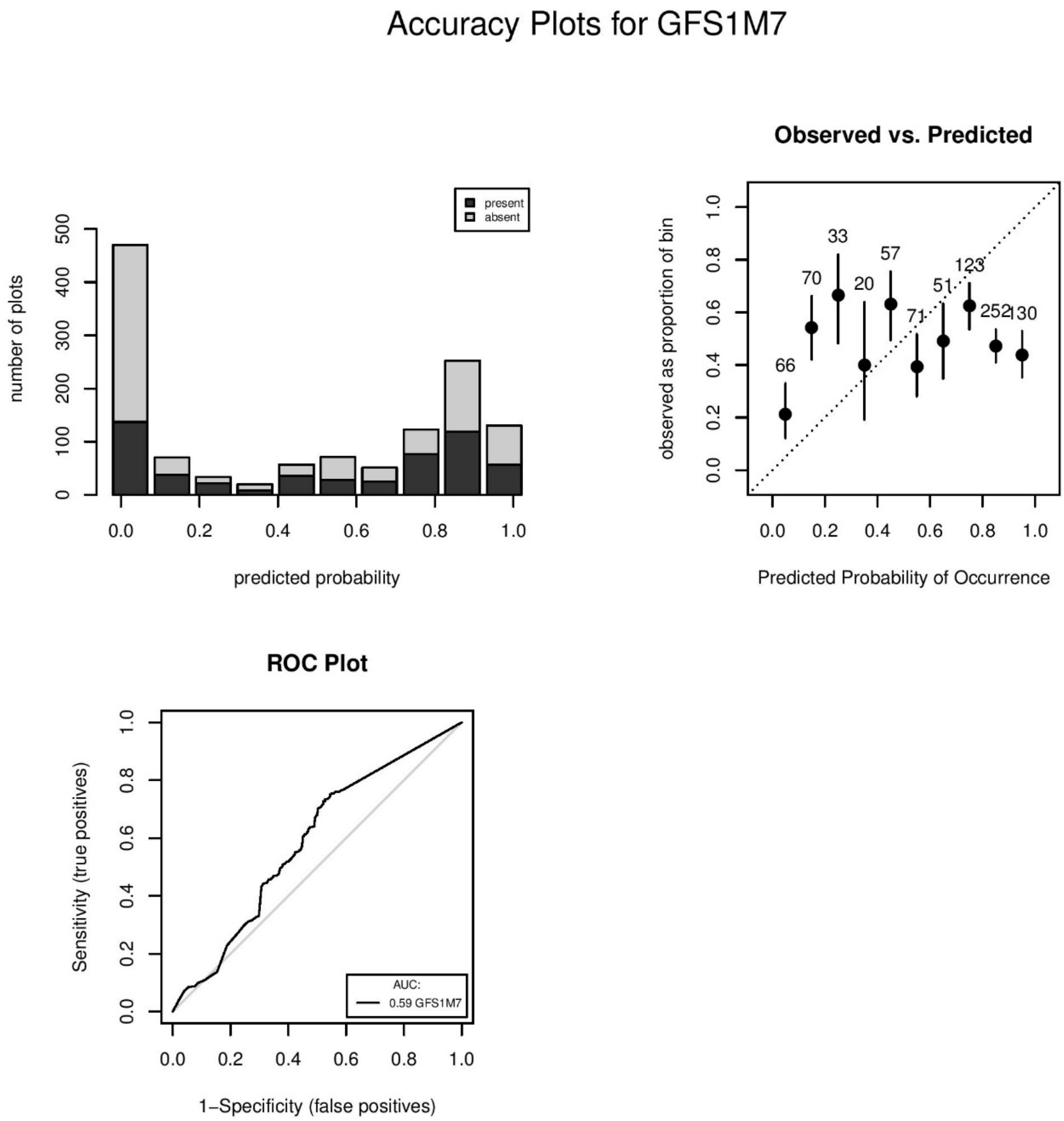
Accuracy Plots for GFS1M4

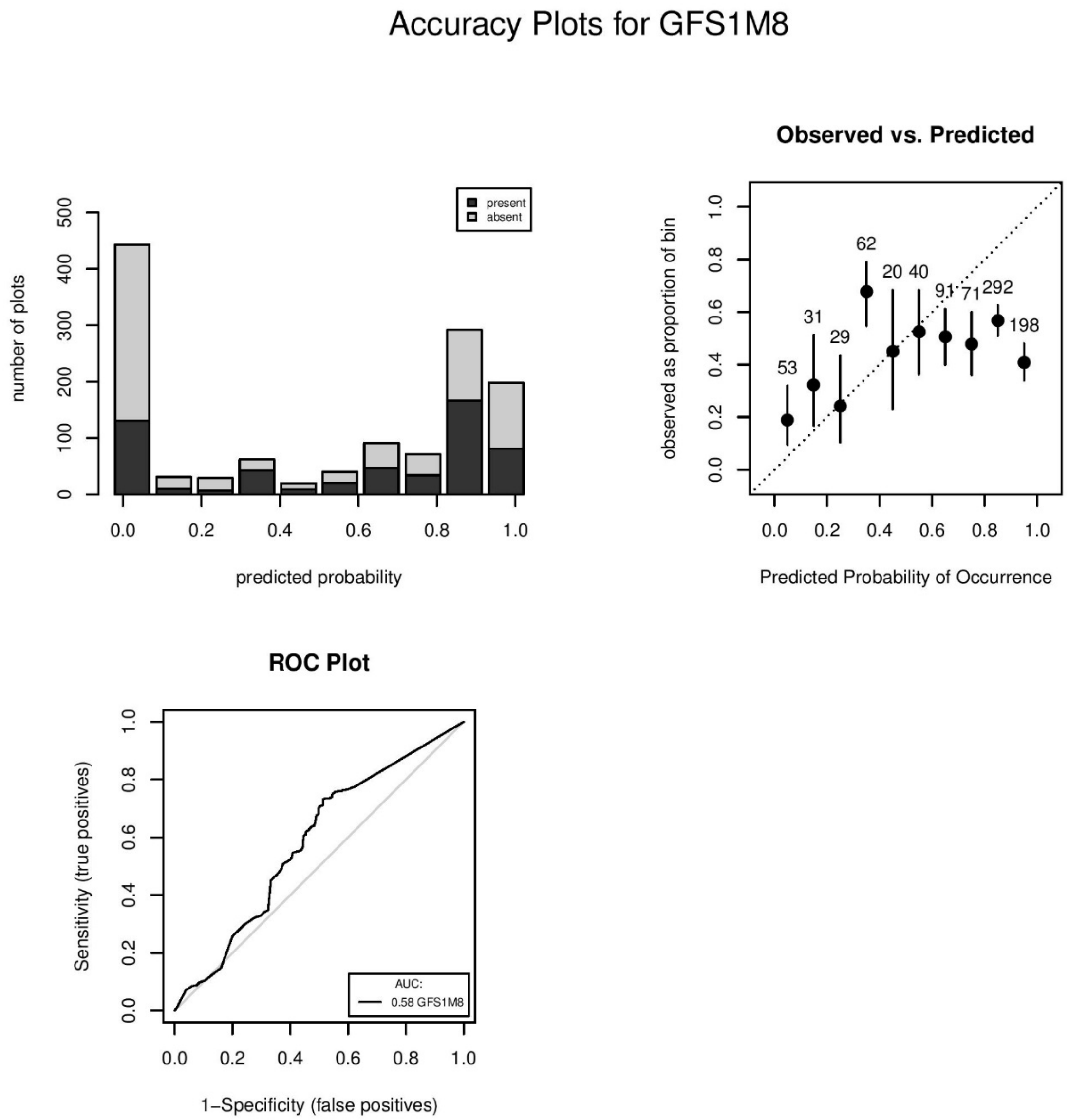


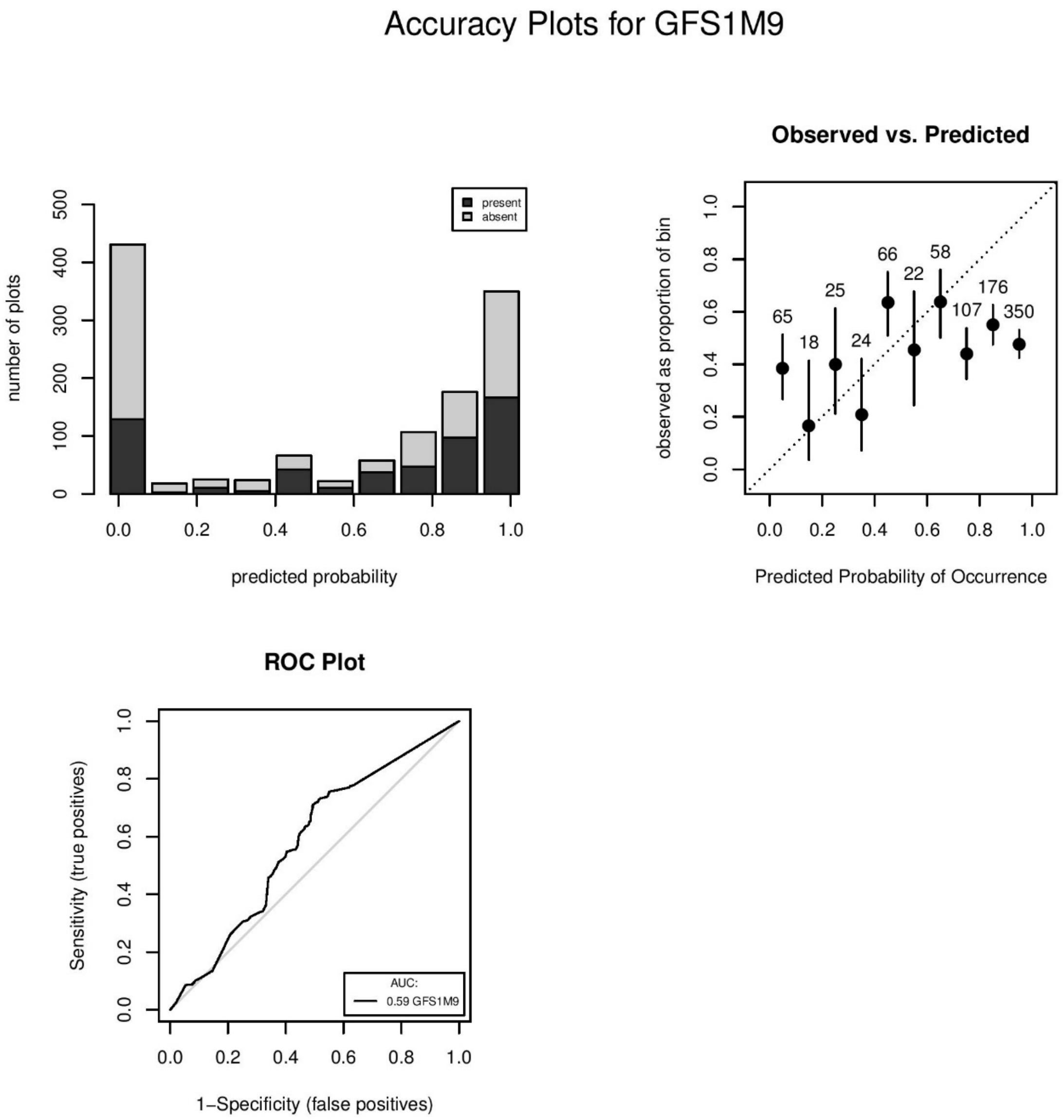


Accuracy Plots for GFS1M5
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
59
38
47
44
29
74
70
131
255
138
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M5

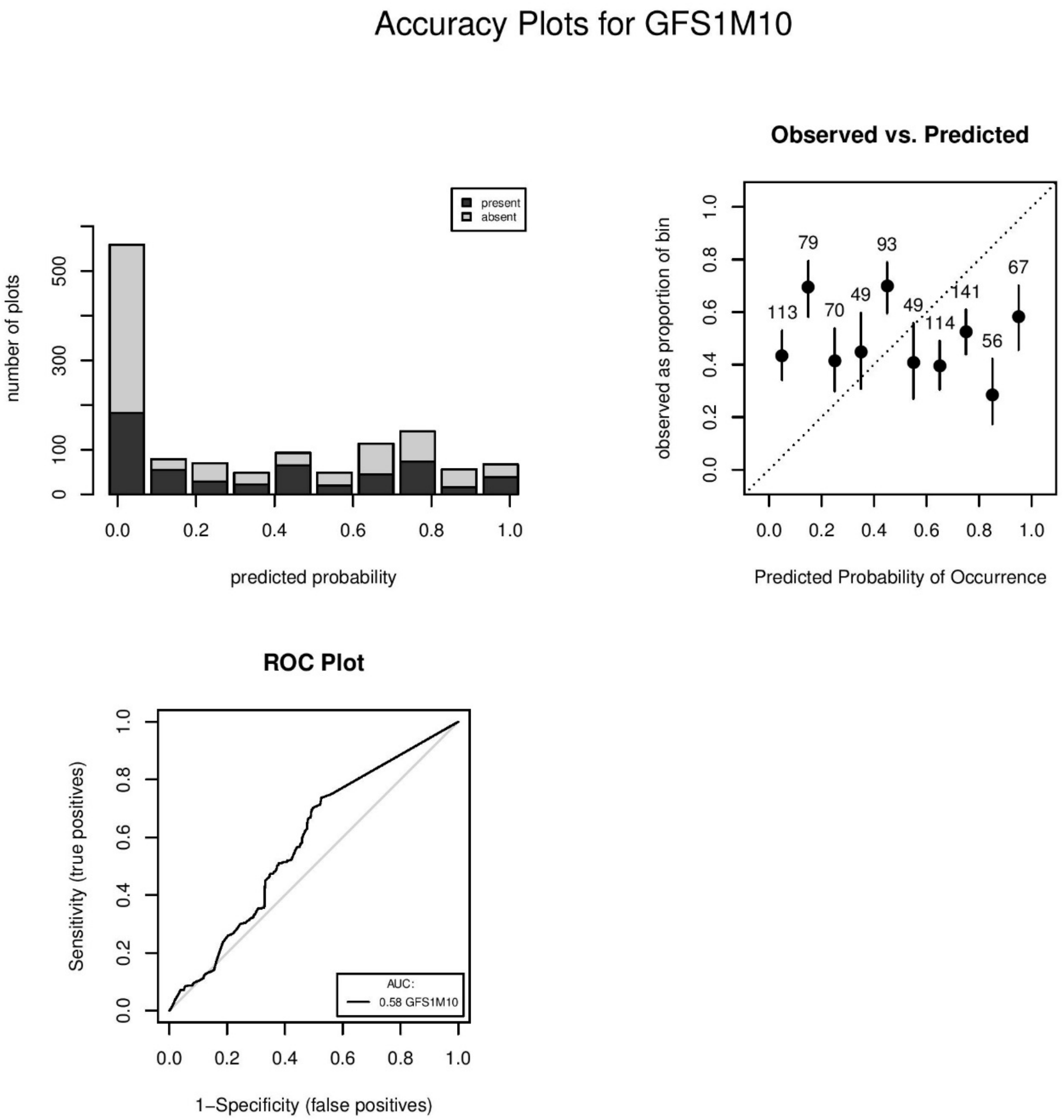

Accuracy Plots for GFS1M6
number of plots
predicted probability
present
absent
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
70 19 29 38 52 31 89 135 252 191
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS1M6


Accuracy Plots for GFS1M7
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
66
70
33
20
57
71
51
123
252
130
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS1M7

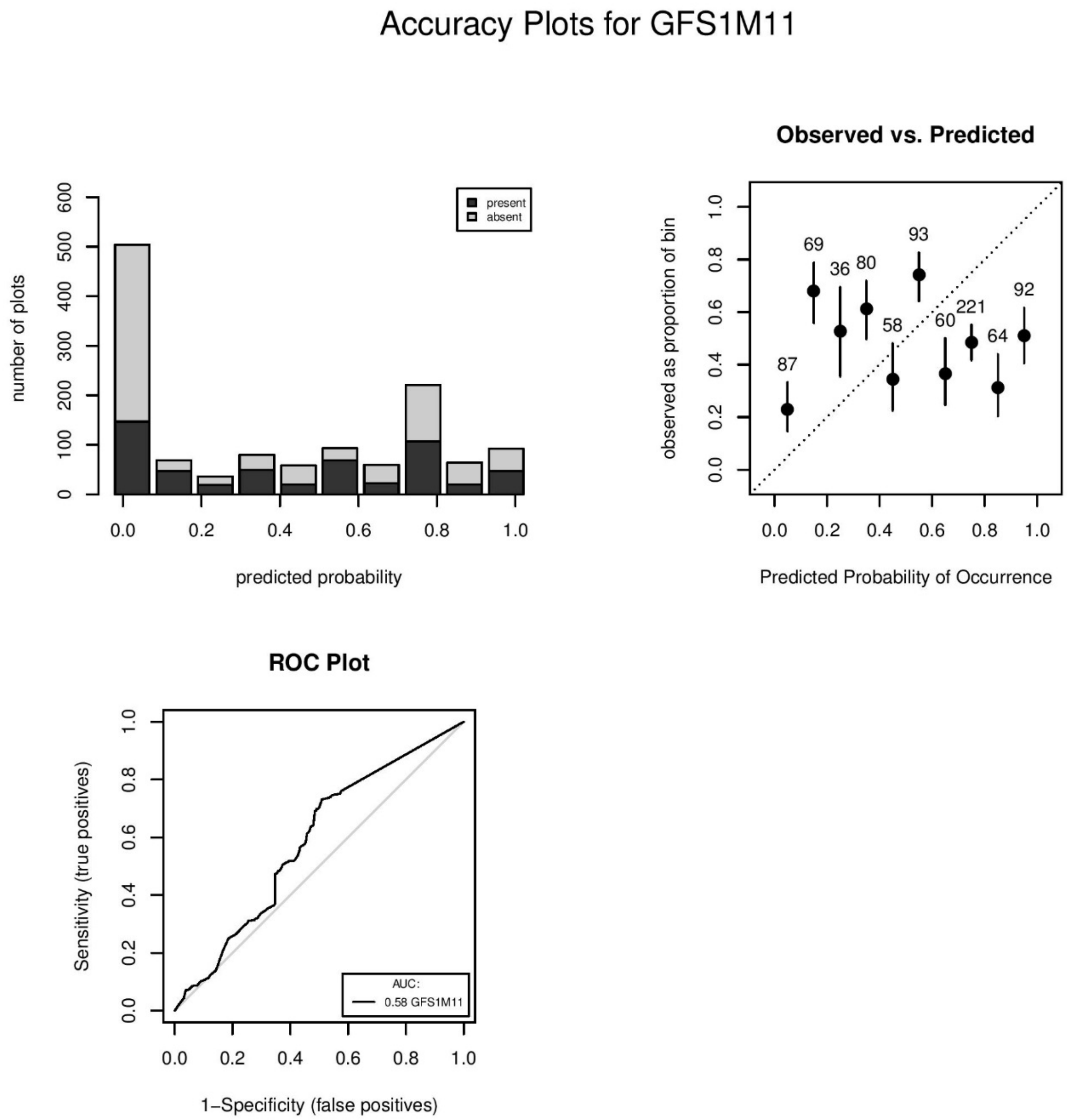

Accuracy Plots for GFS1M8
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
53
31
29
62
20 40
91
71
292
198
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M8



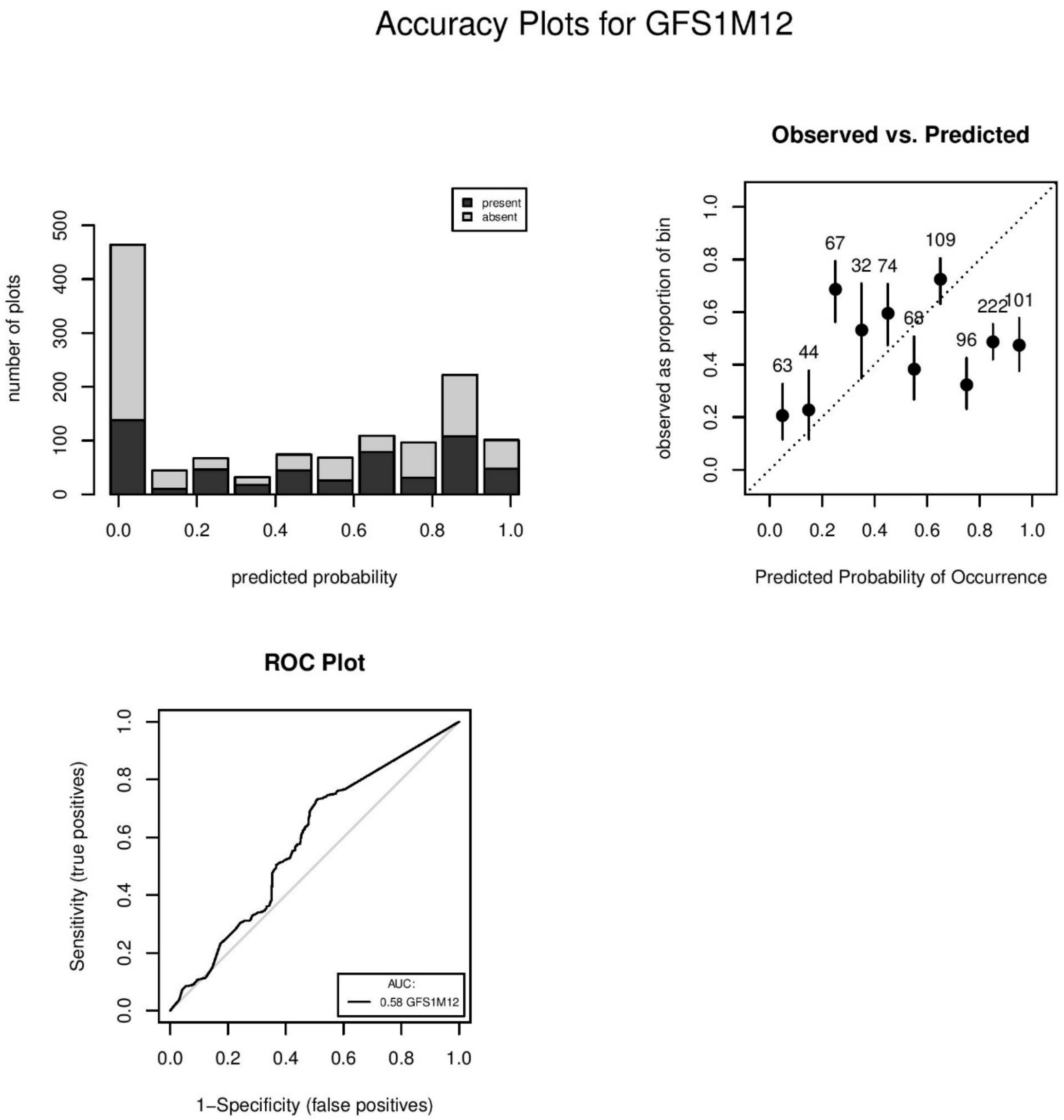
Accuracy Plots for GFS1M9
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
65
18
25
24
66
22
58
107
176
350
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS1M9



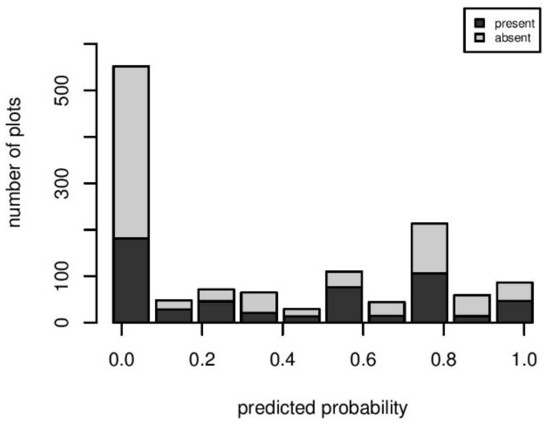
Accuracy Plots for GFS1M10
present
absent
number of plots
0
100
300
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
113
79
70
49
93
49
114
141
56
67
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M10

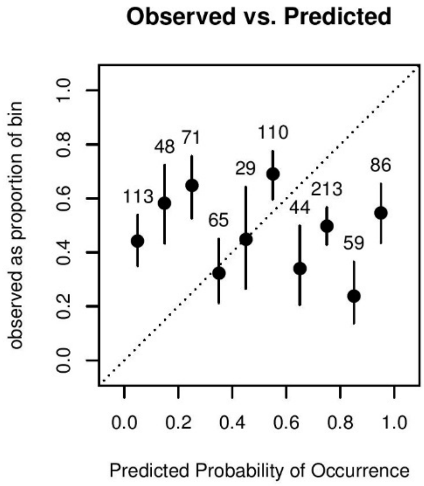


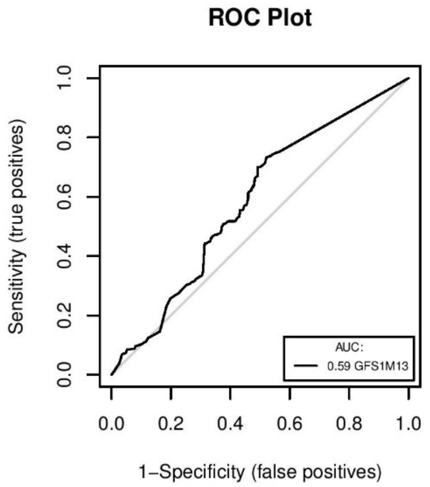
Accuracy Plots for GFS1M11
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
87
69
36
80
58
93
60
221
64
92
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M11

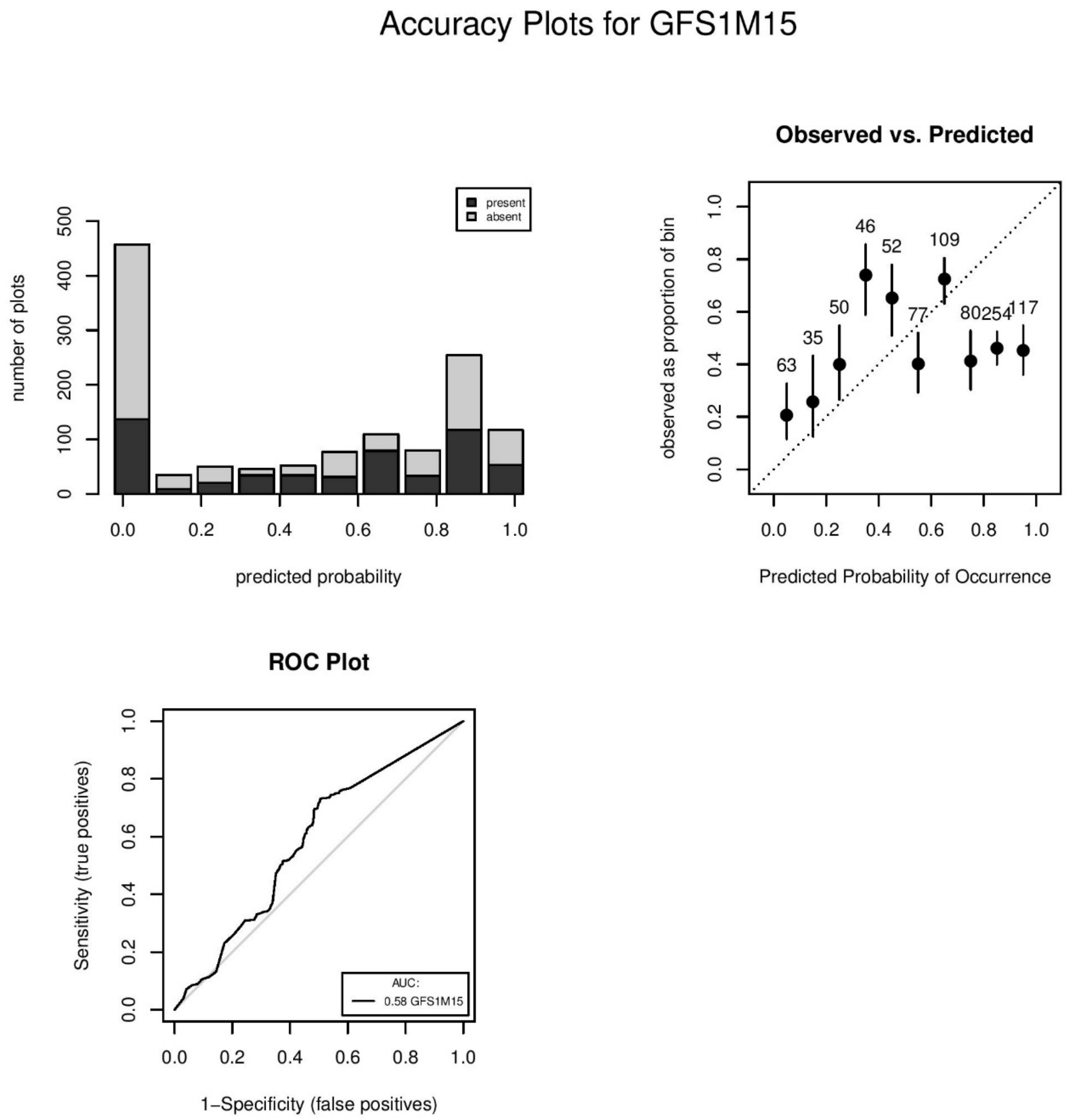

Accuracy Plots for GFS1M12
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
63
44
67
32 74
68
109
96
222
101
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M12

Accuracy Plots for GFS1M13

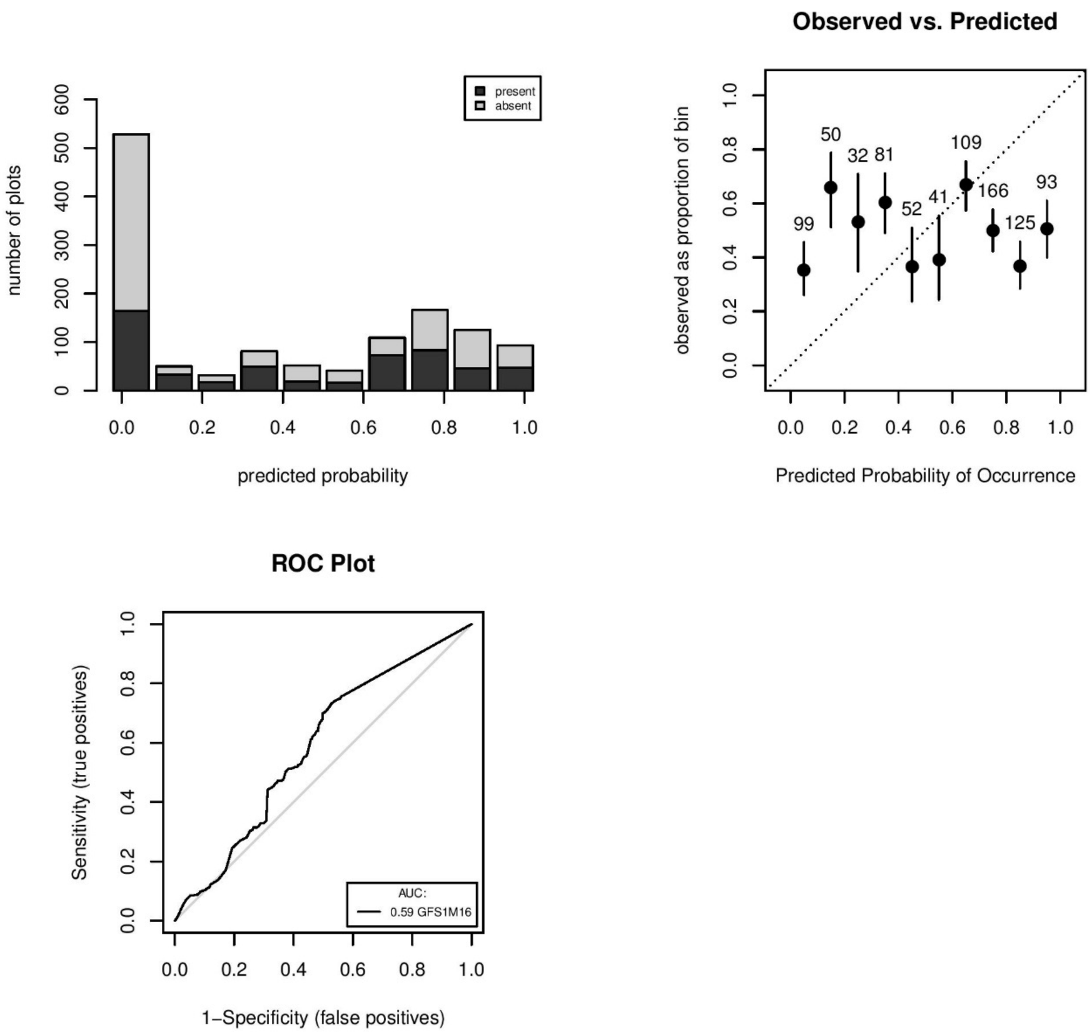


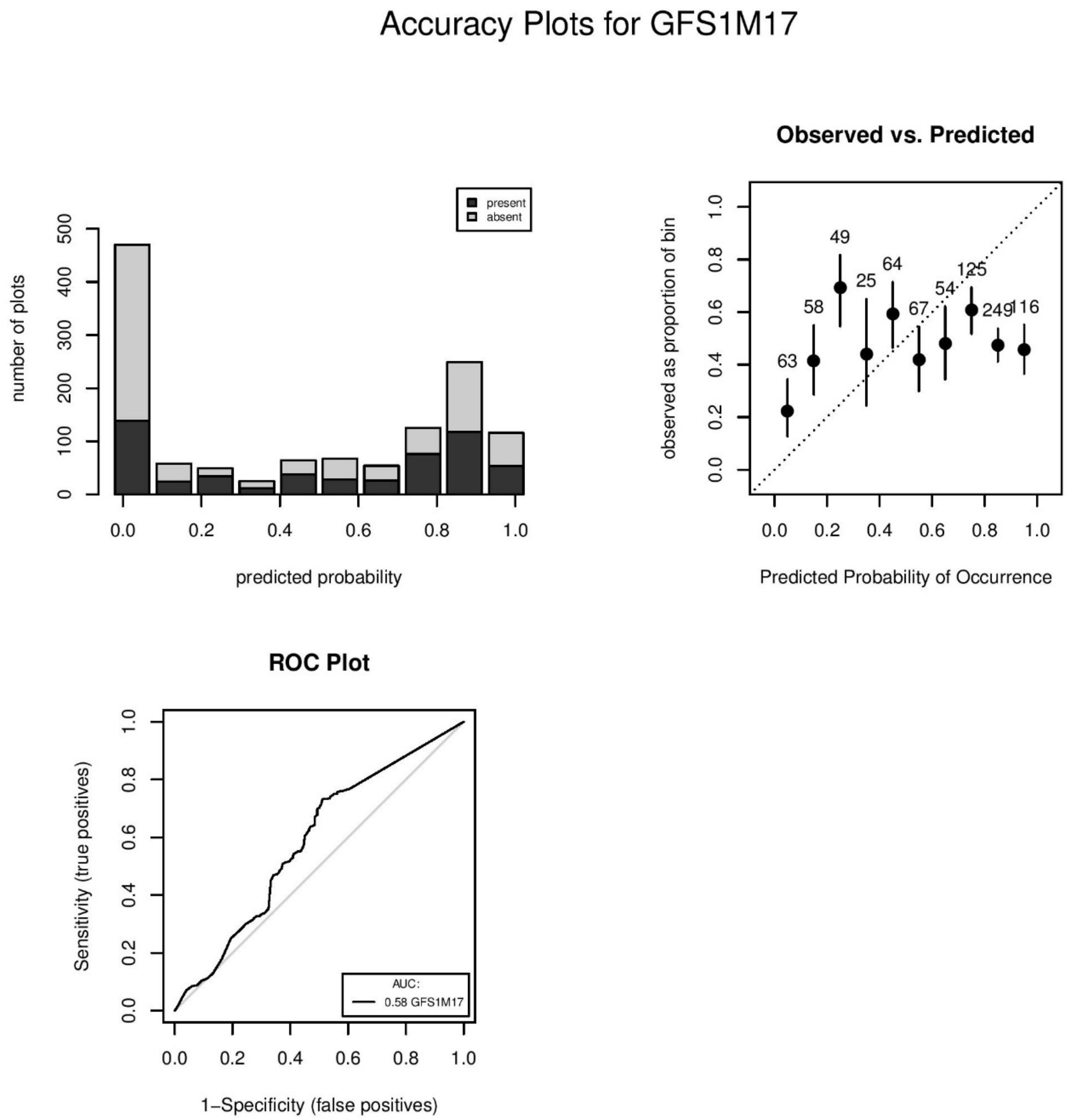


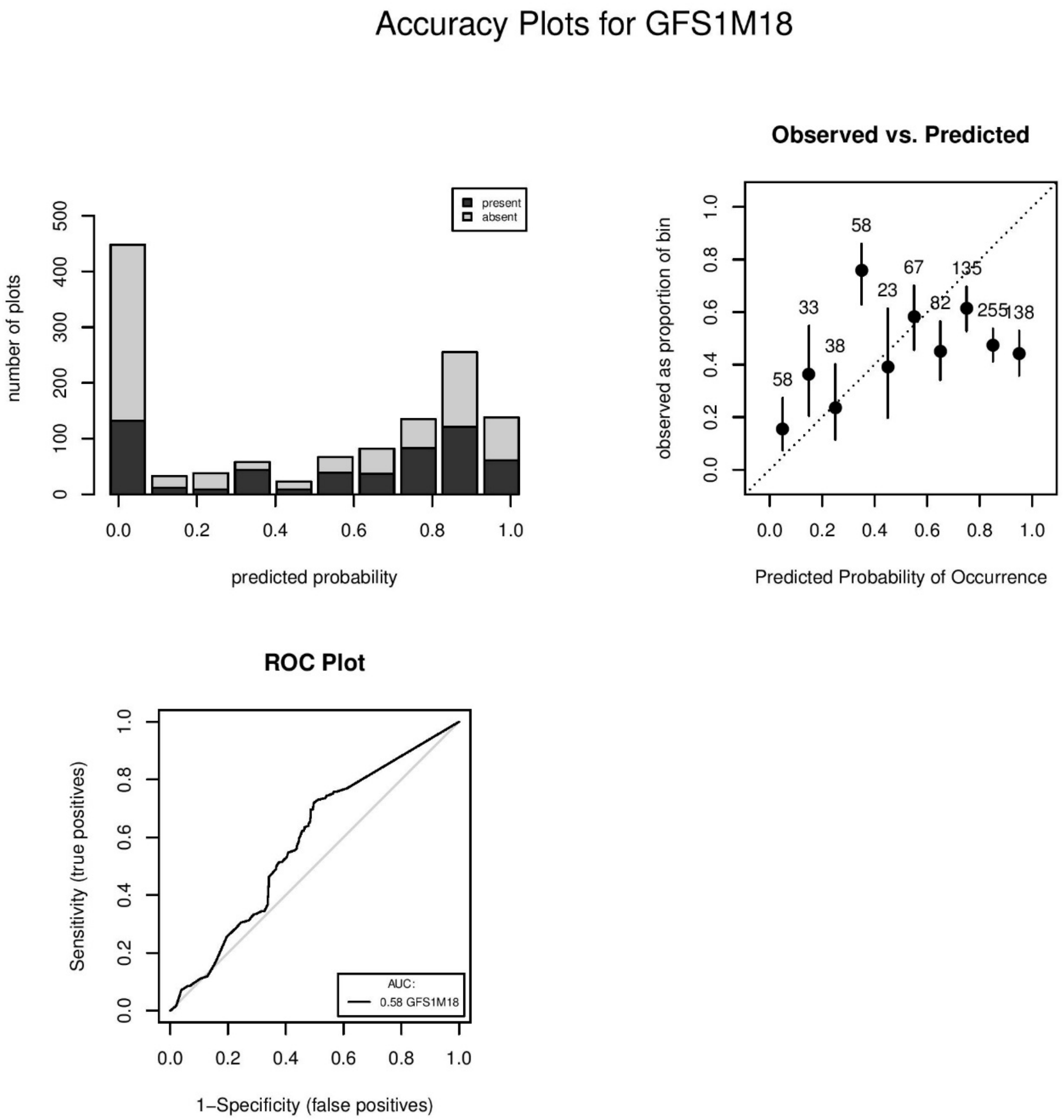


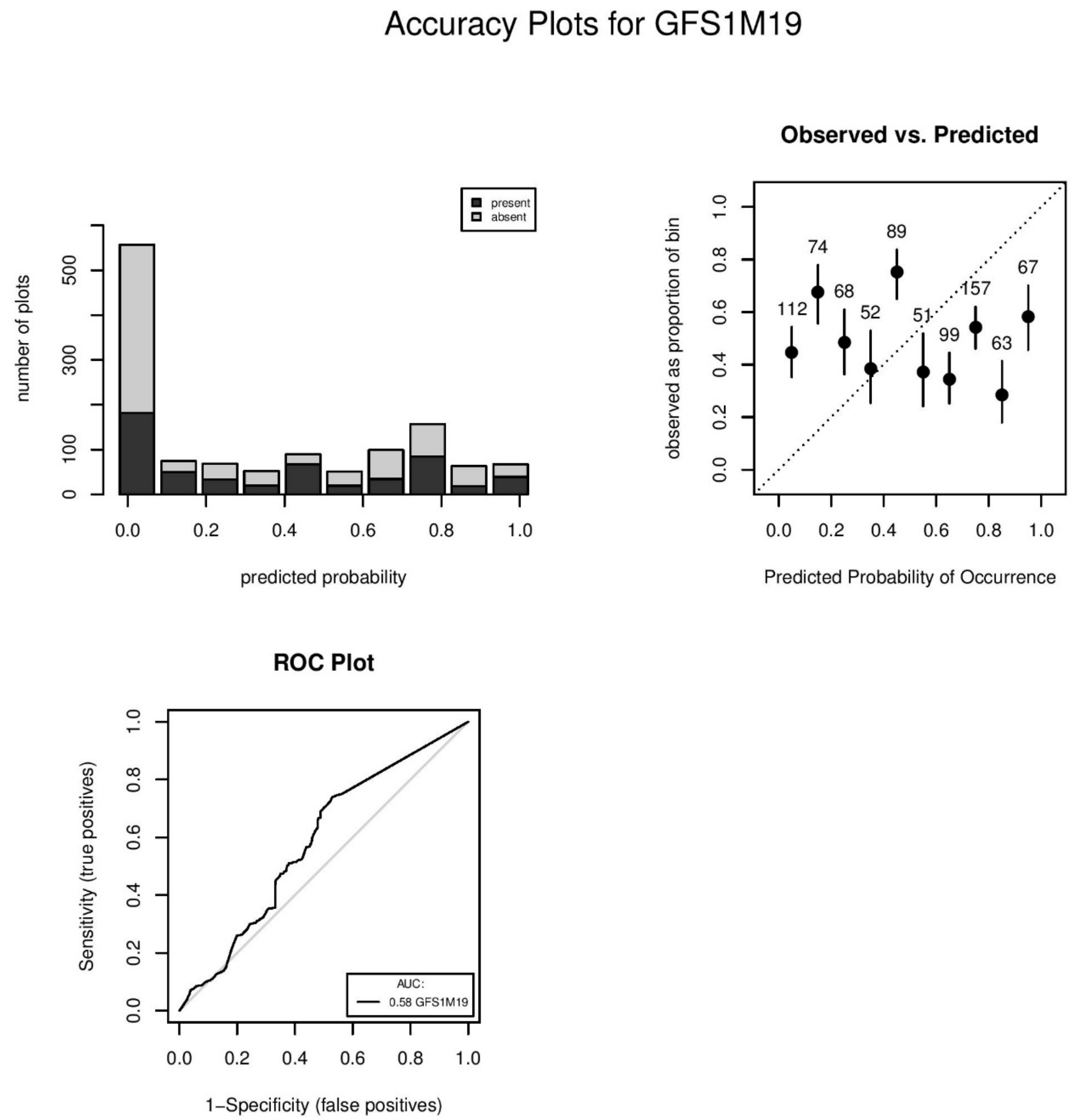

Accuracy Plots for GFS1M15
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
63
35
50
46
52
77
109
80
254
117
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M15

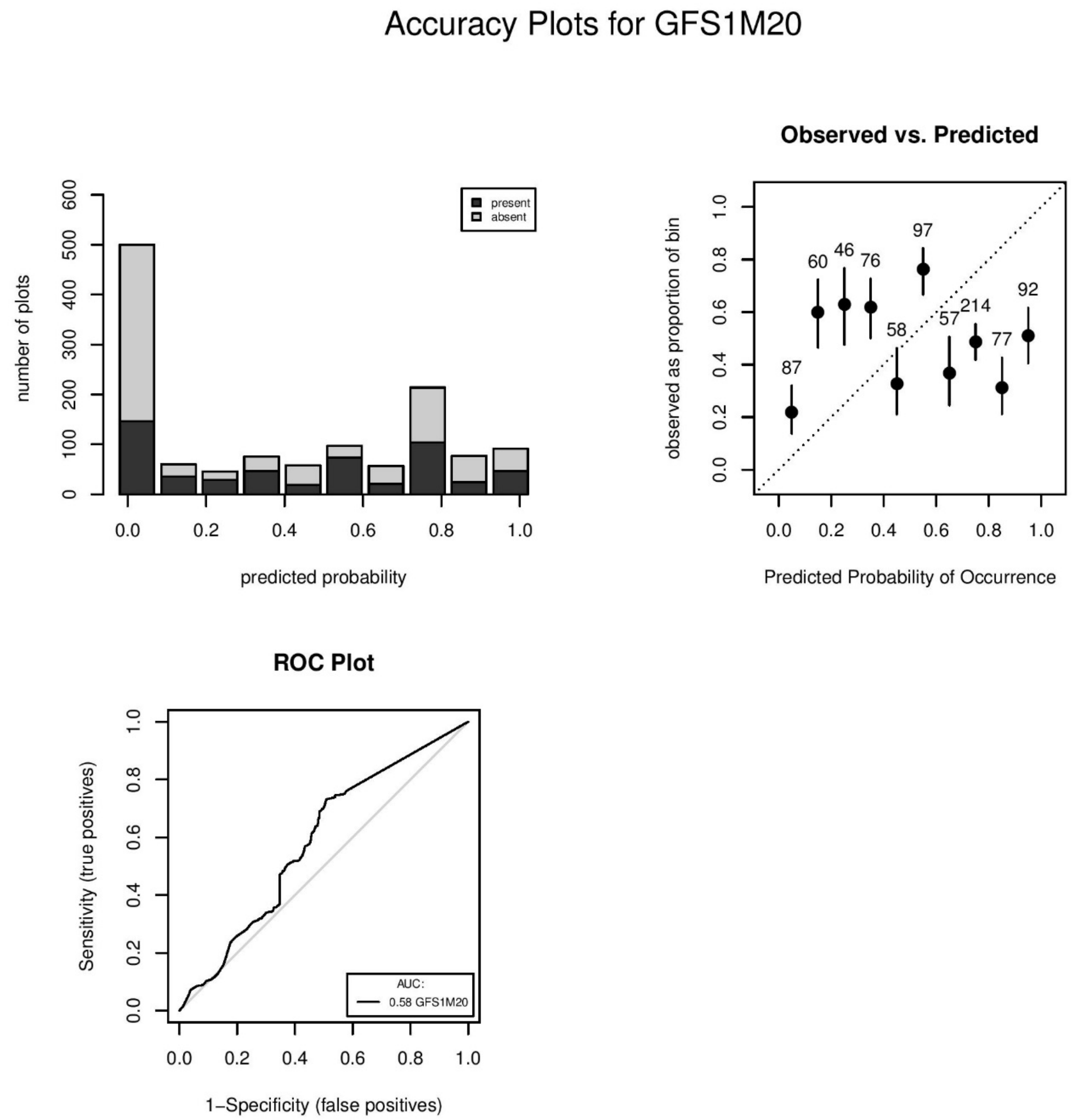
Accuracy Plots for GFS1M16

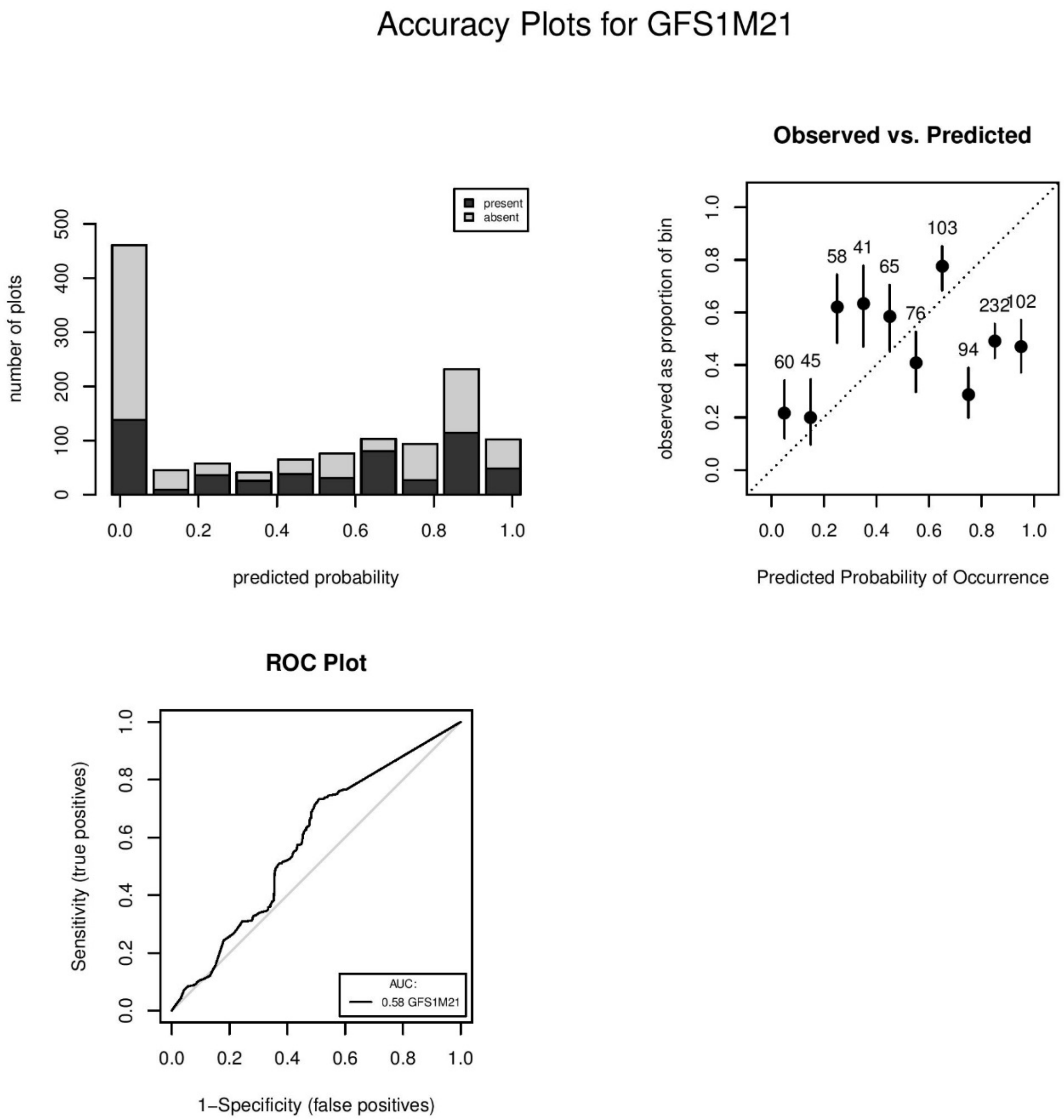



Accuracy Plots for GFS1M17
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
63
58
49
25
64
67
54
125
249
116
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M17

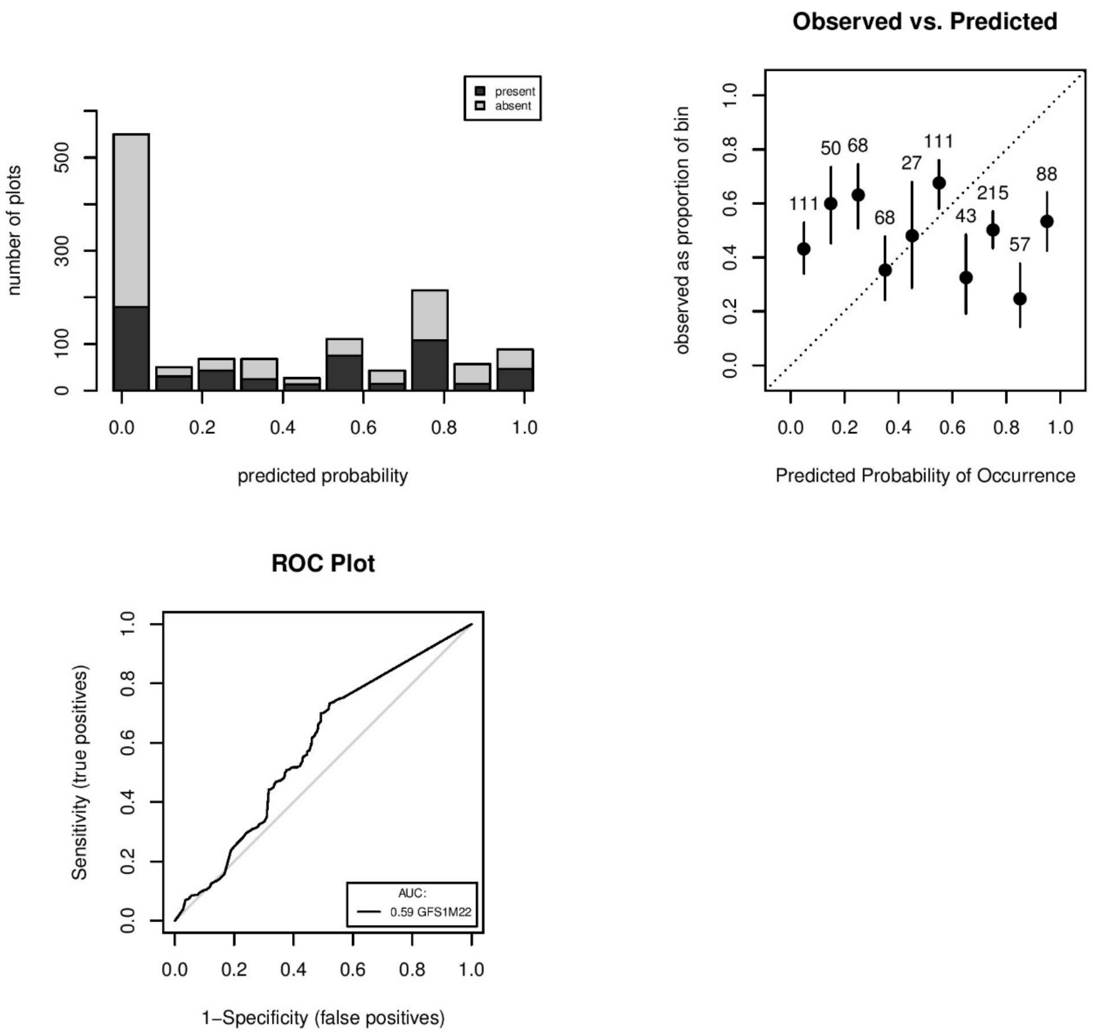

Accuracy Plots for GFS1M18
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
58
33
38
58
23
67
82
135
255
138
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M18

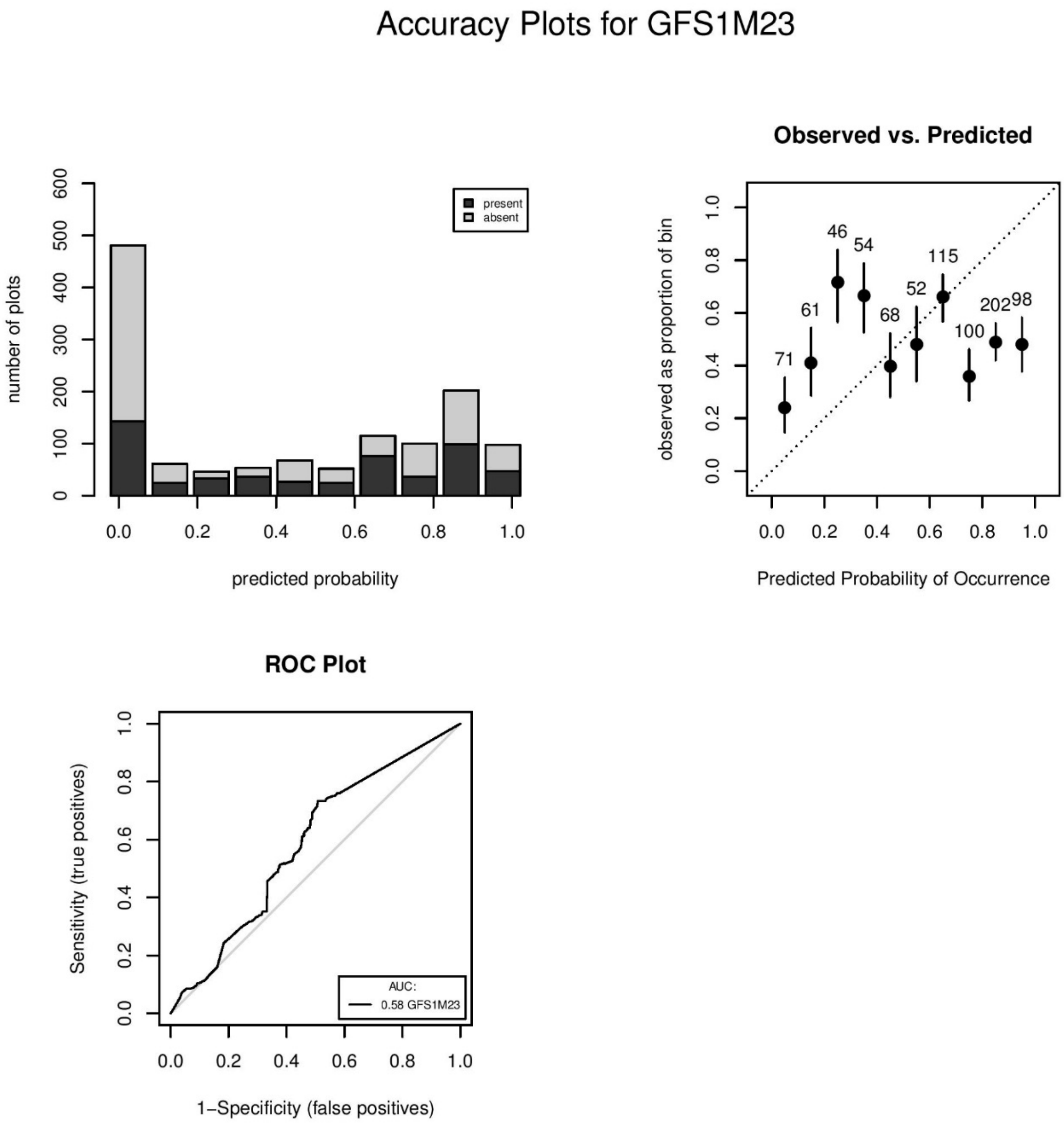

Accuracy Plots for GFS1M19
present
absent
number of plots
0
100
300
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
112
74
68
52
89
51
99
157
63
67
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M19


Accuracy Plots for GFS1M20
present
absent
number of plots
predicted probability
0
100
200
300
400
500
600
0.0
0.2
0.4
0.6
0.8
1.0
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
87
60
46
76
58
97
57
214
77
92
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M20

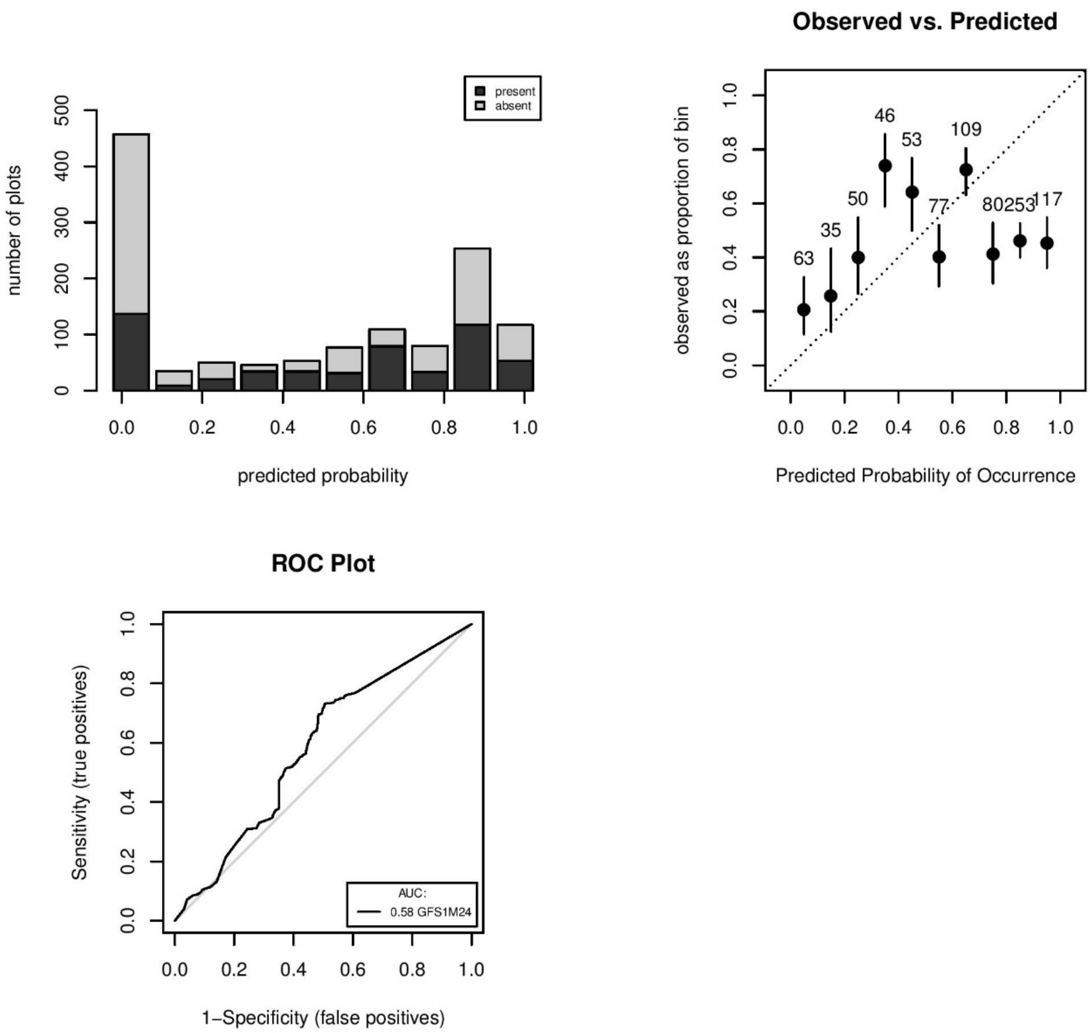

Accuracy Plots for GFS1M21
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
60
45
58
41
65
76
103
94
232
102
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M21

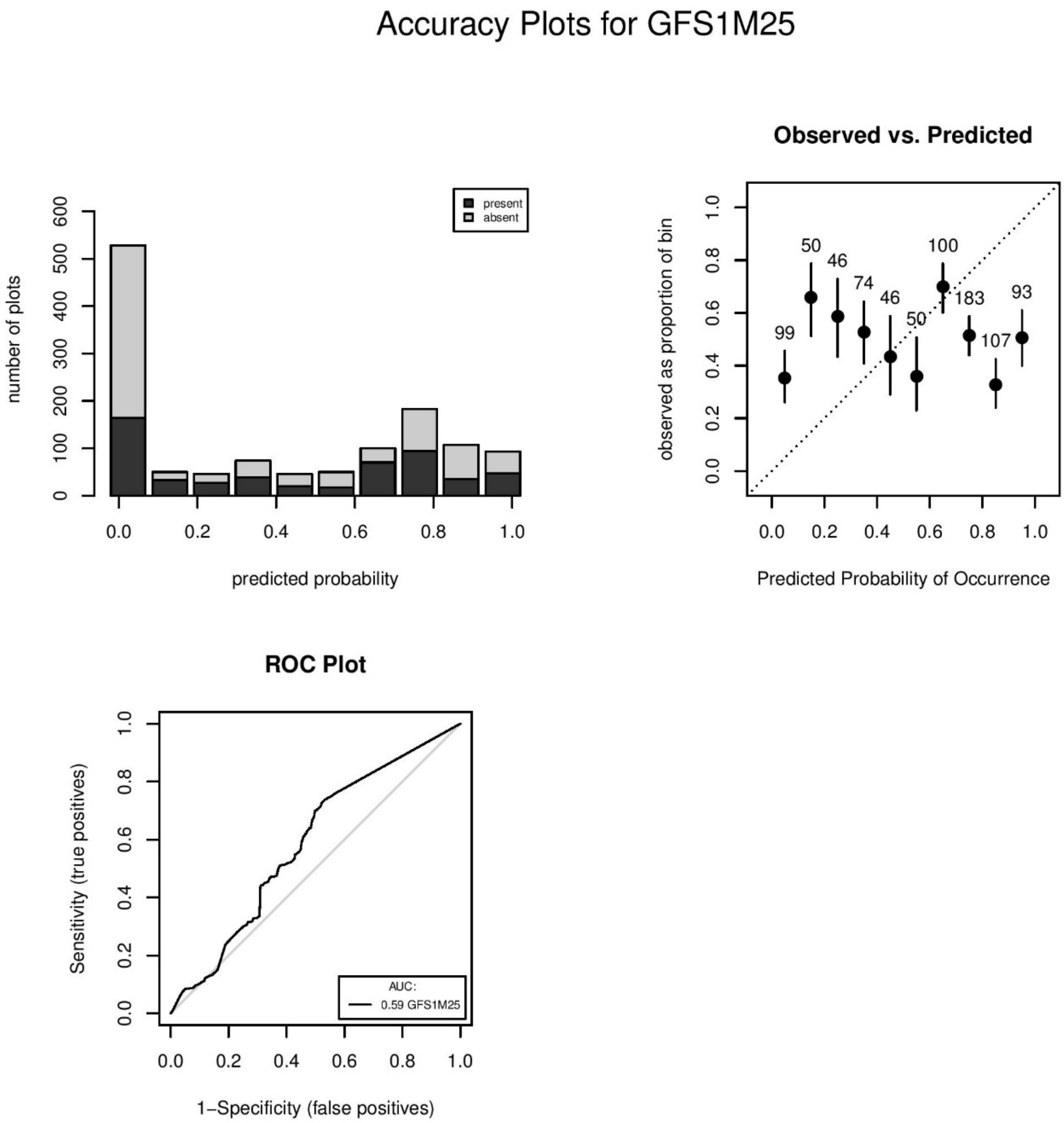
Accuracy Plots for GFS1M22

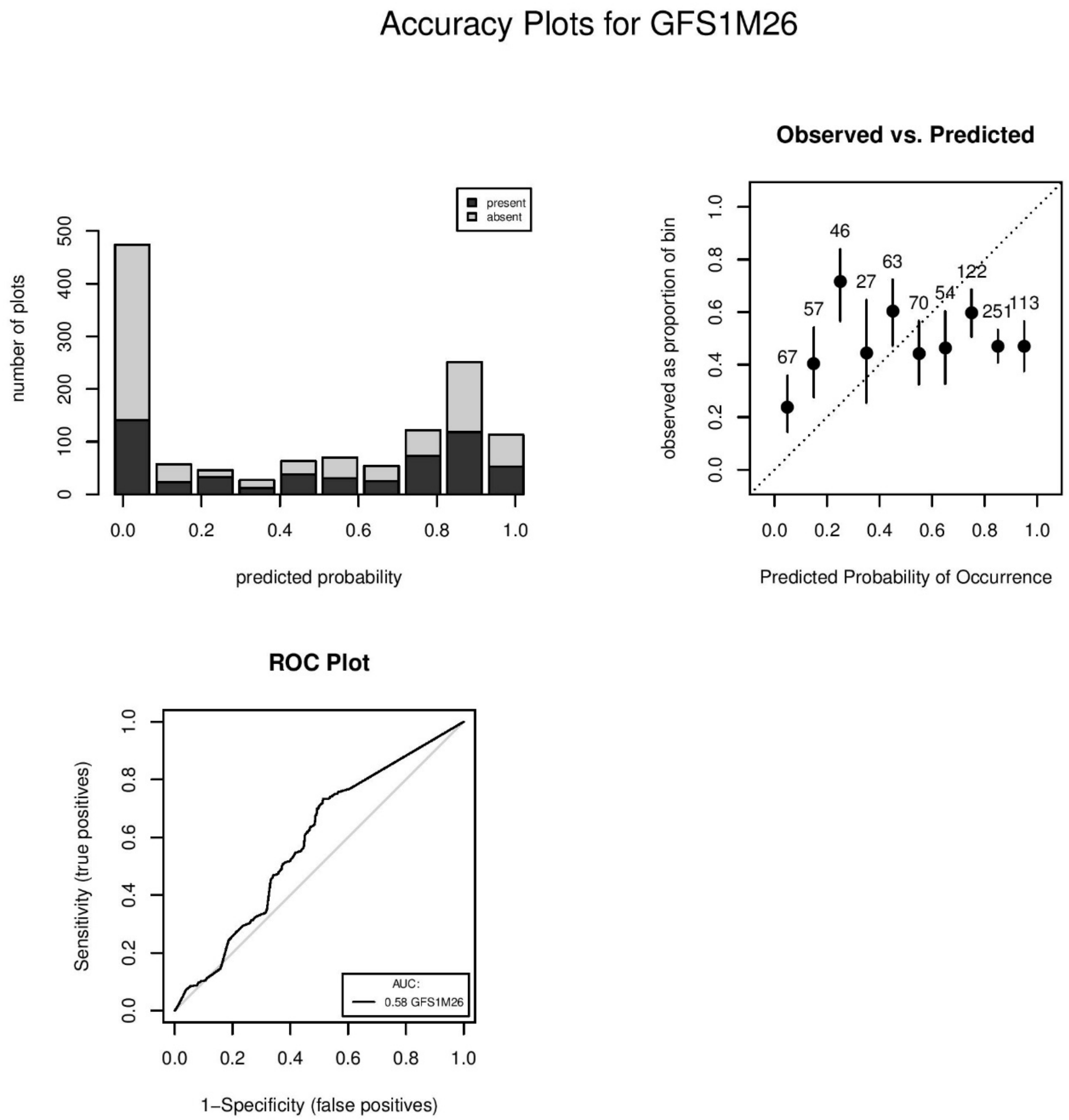


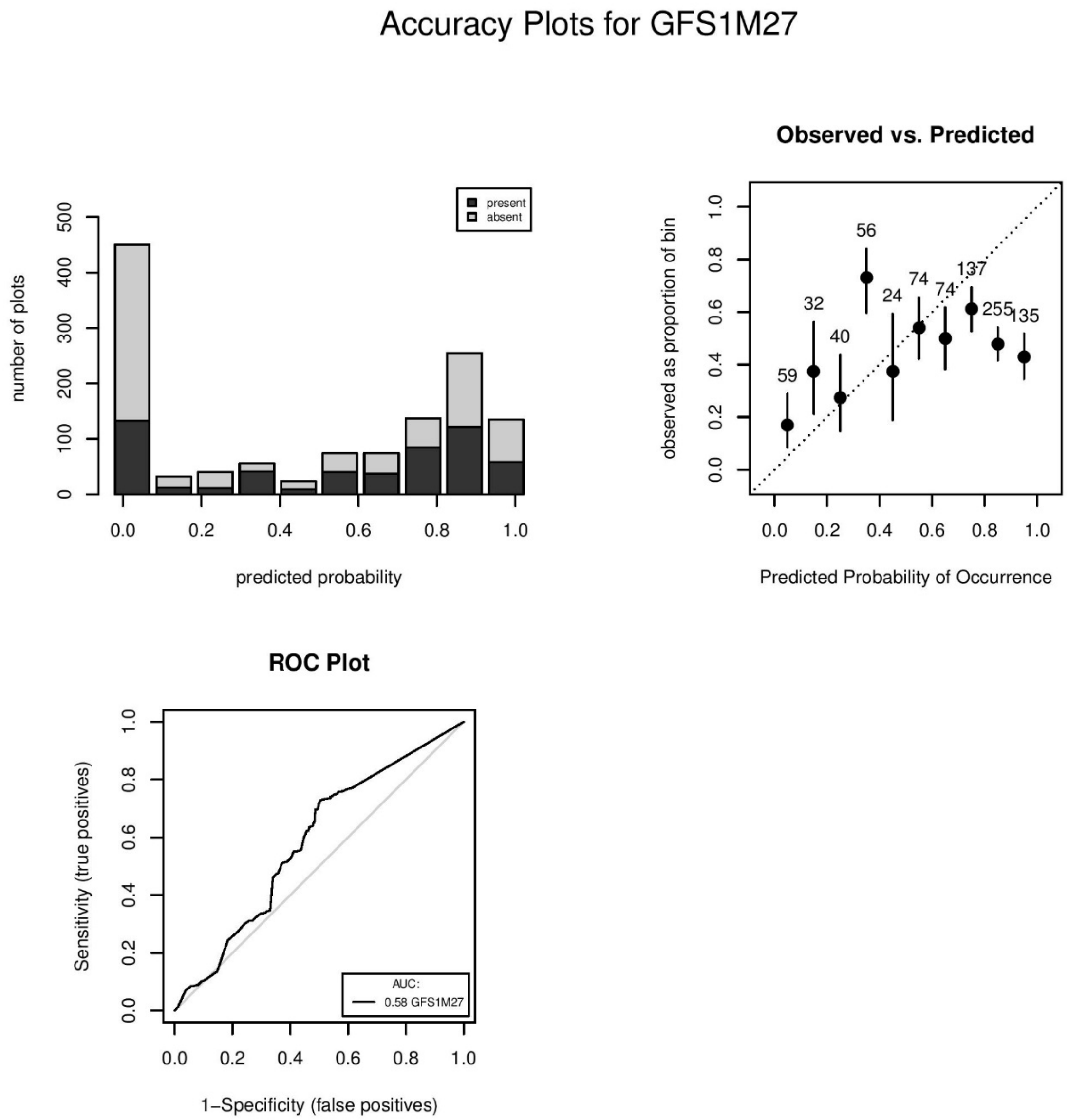

Accuracy Plots for GFS1M23
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
71
61
46
54
68
52
115
100
202
98
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M23

Accuracy Plots for GFS1M24

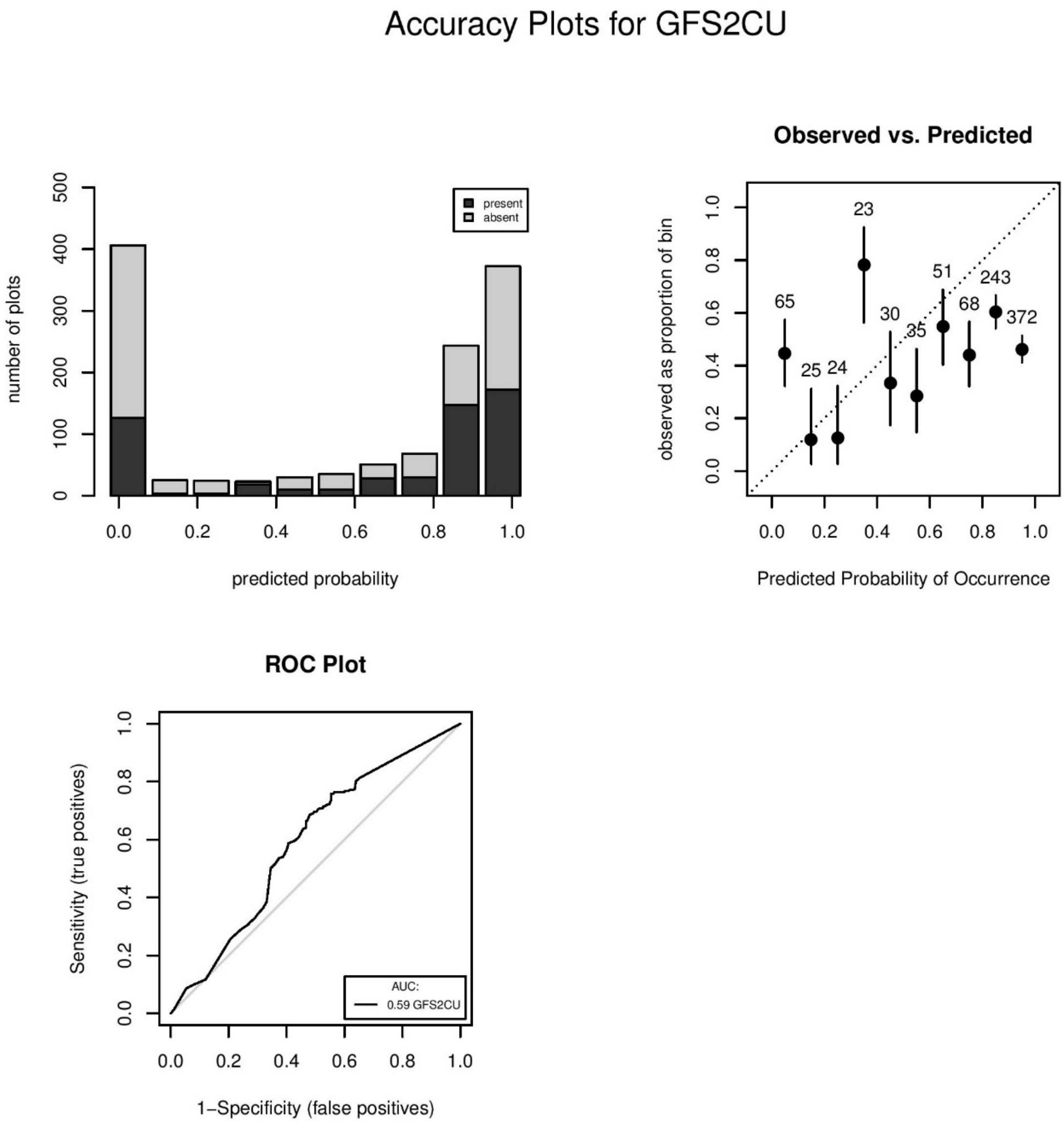


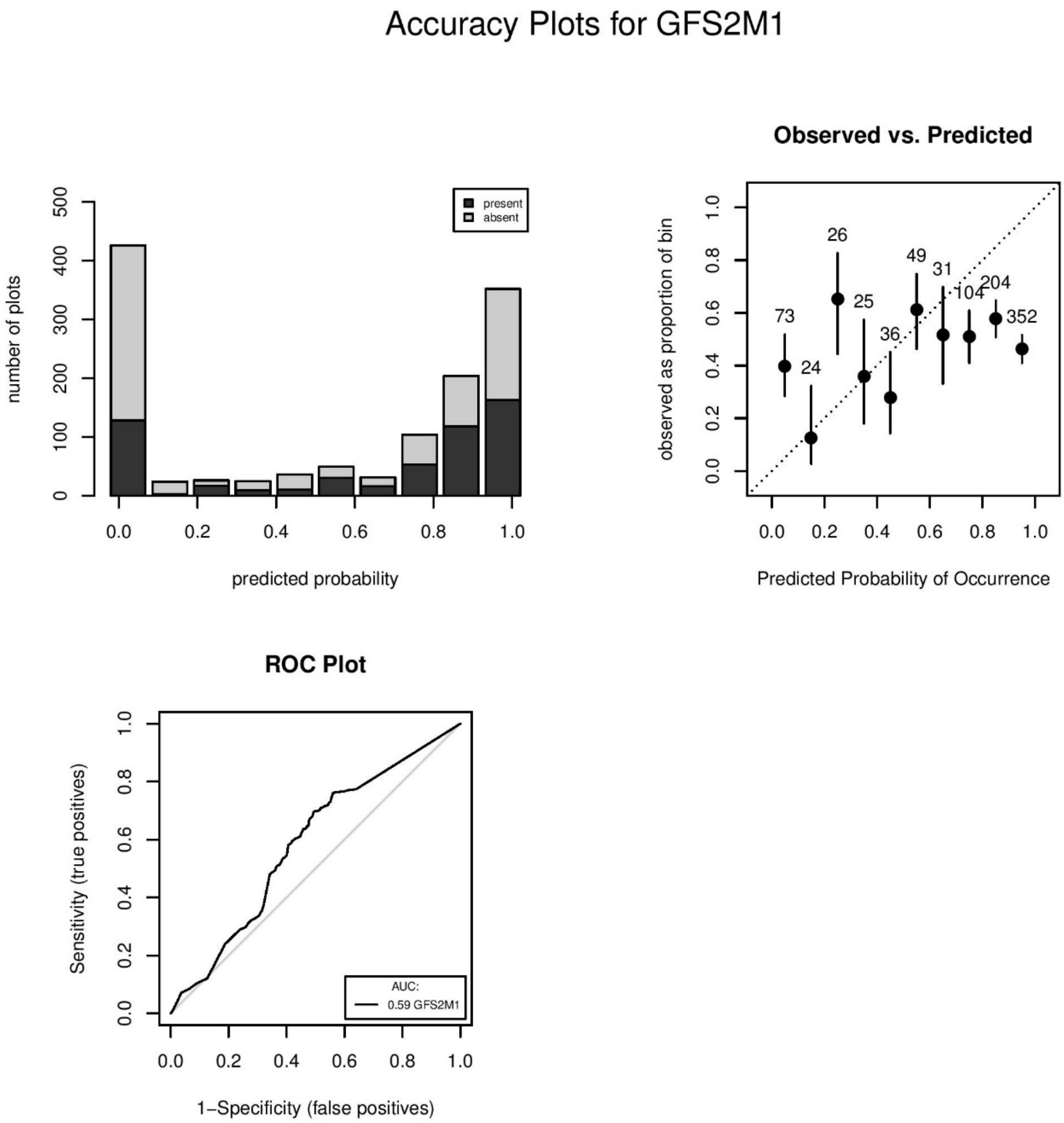

Accuracy Plots for GFS1M25
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
99
50
46
74
46
50
100
183
107
93
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS1M25

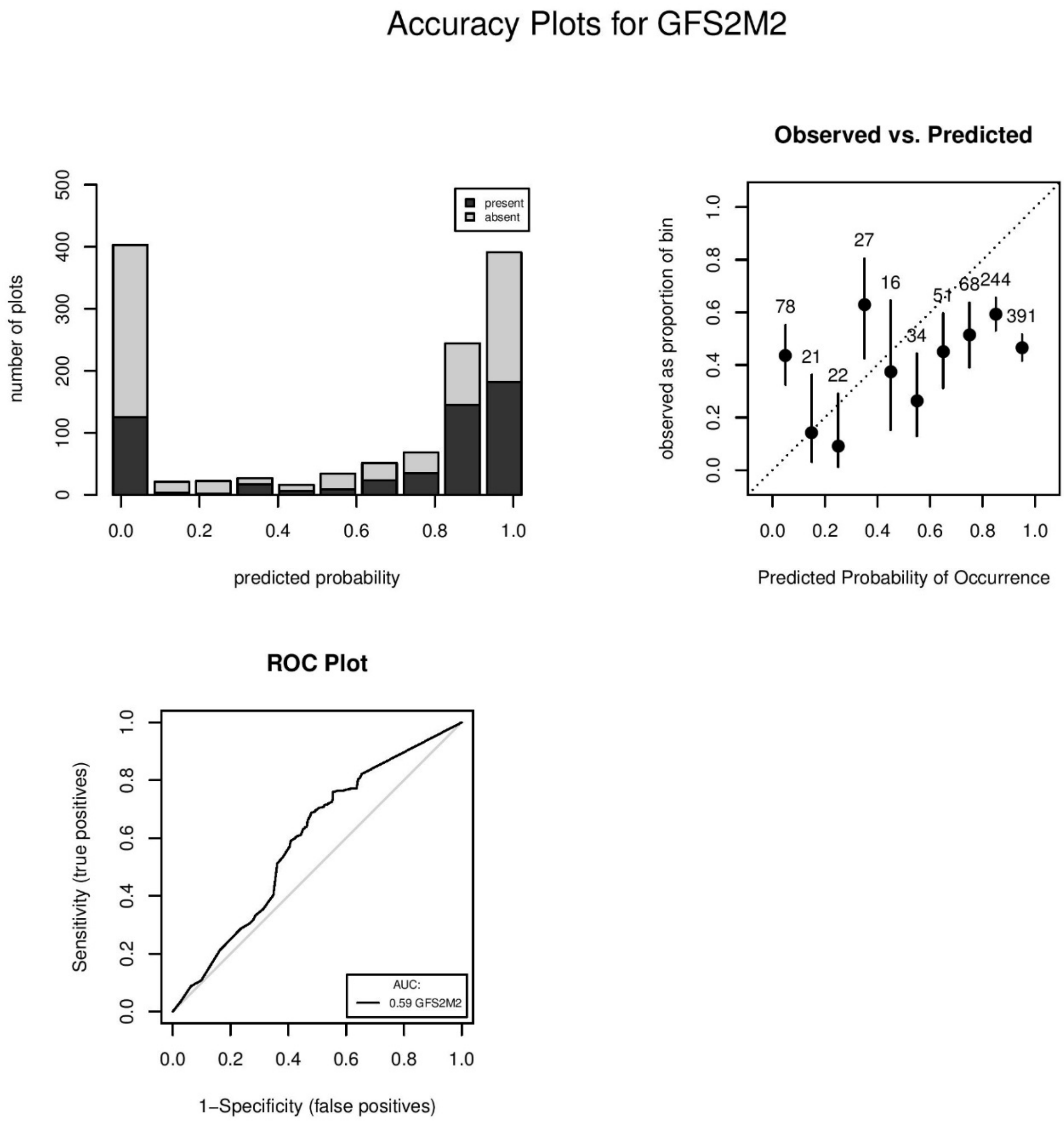

Accuracy Plots for GFS1M26
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
67
57
46
27
63
70
54
122
251
113
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M26

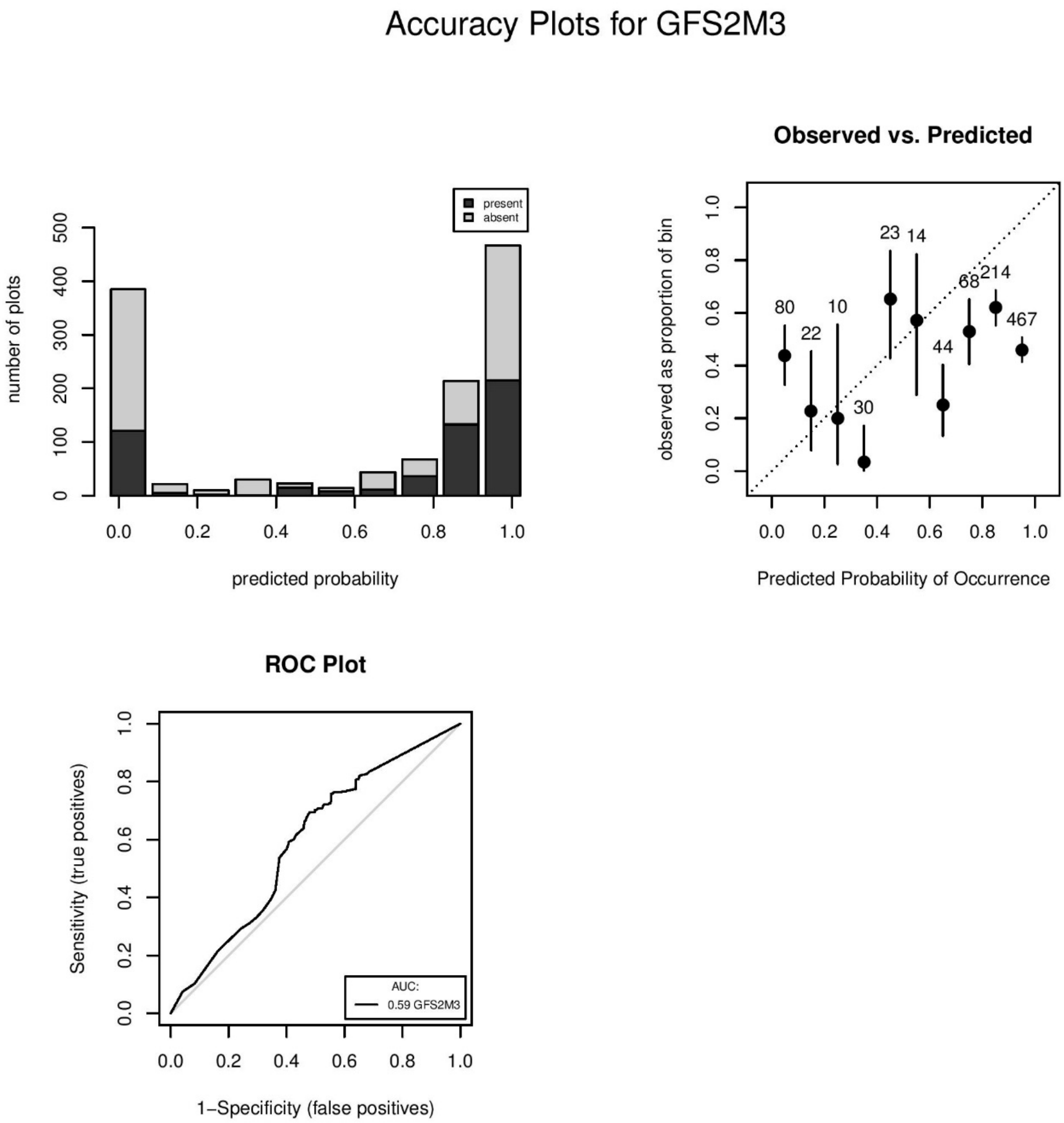


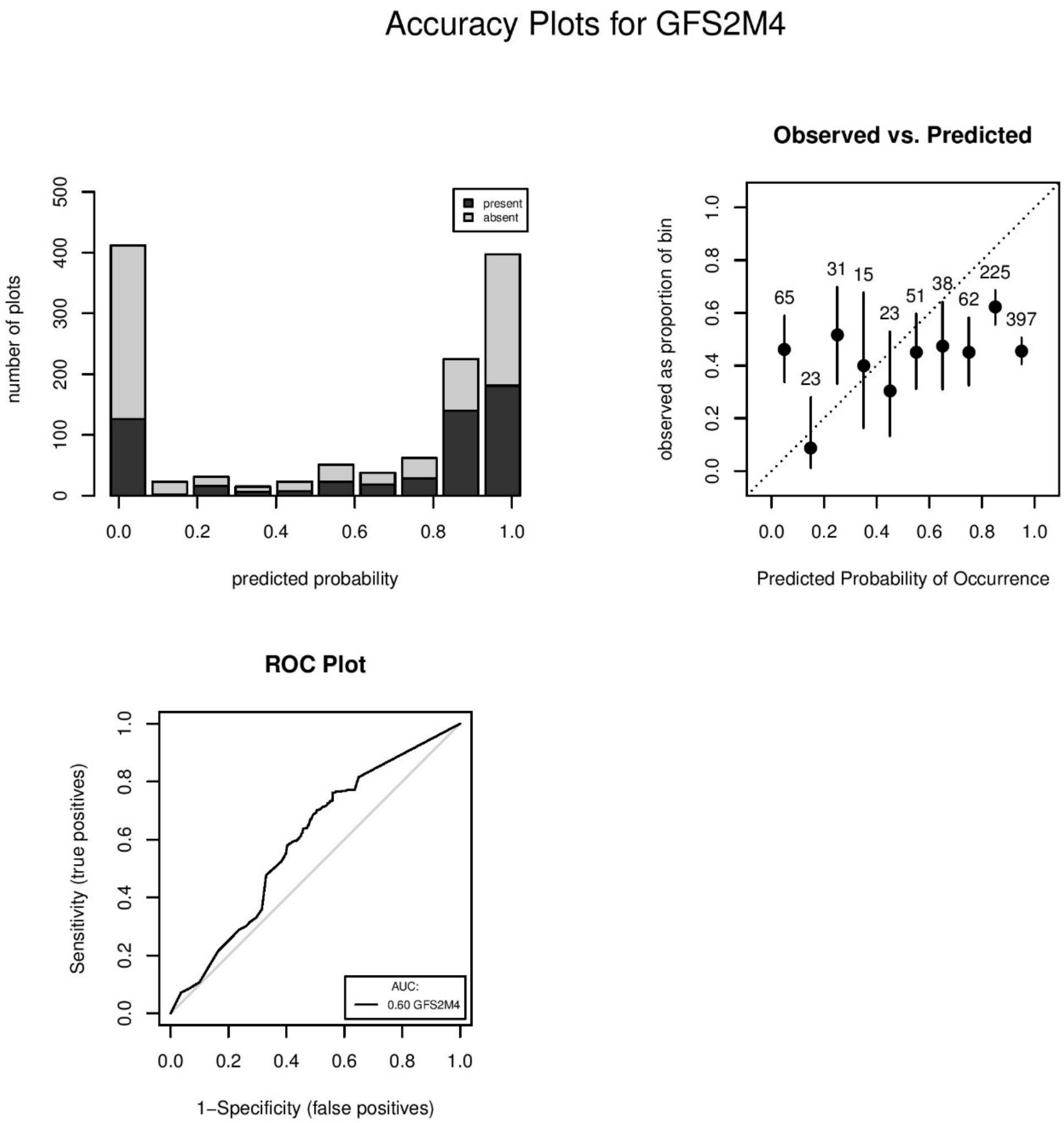
Accuracy Plots for GFS1M27
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
59
32
40
56
24
74
74
137
255
135
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M27


Accuracy Plots for GFS2CU
number of plots
predicted probability
present
absent
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
65
25
24
23
30
35
51
68
243
372
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2CU

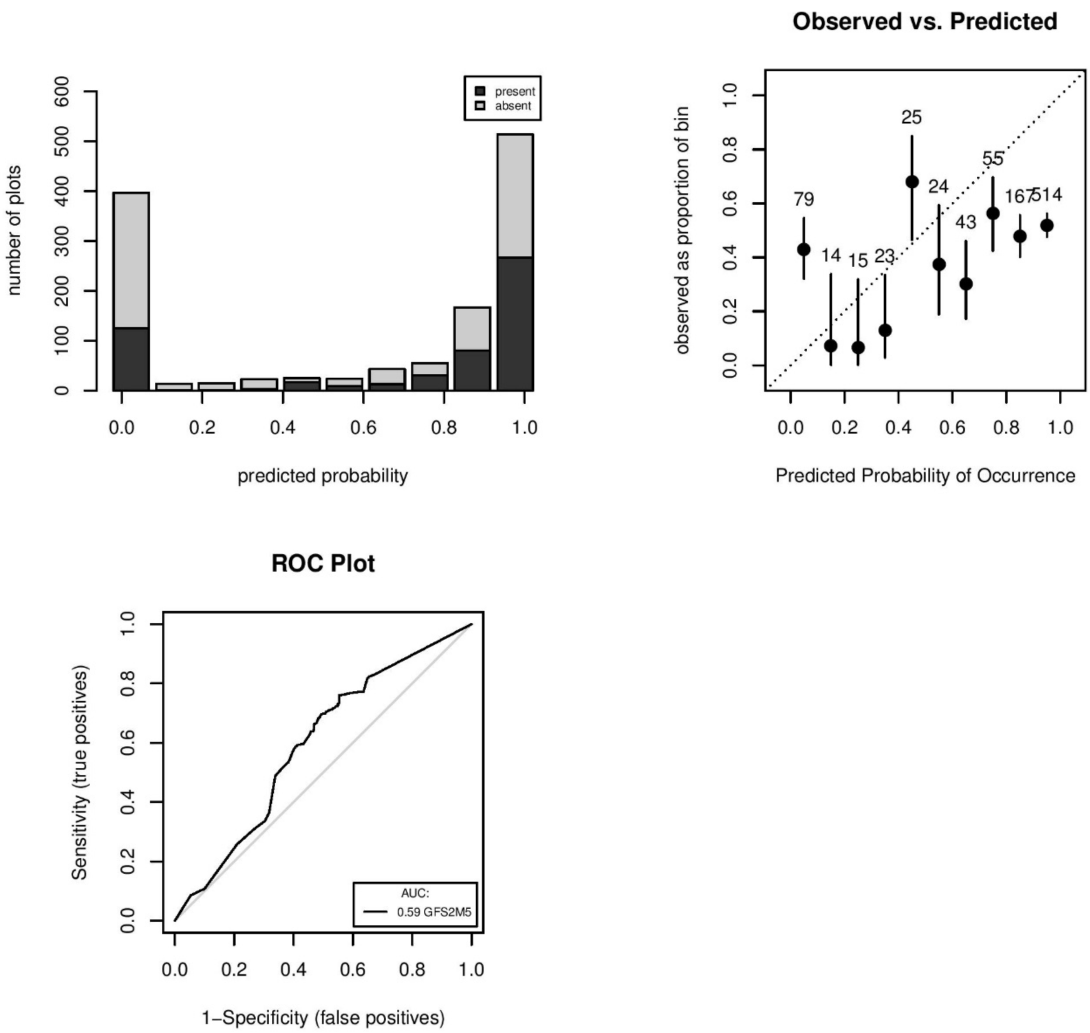

Accuracy Plots for GFS2M1
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
73
24
26
25
36
49
31
104
204
352
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M1

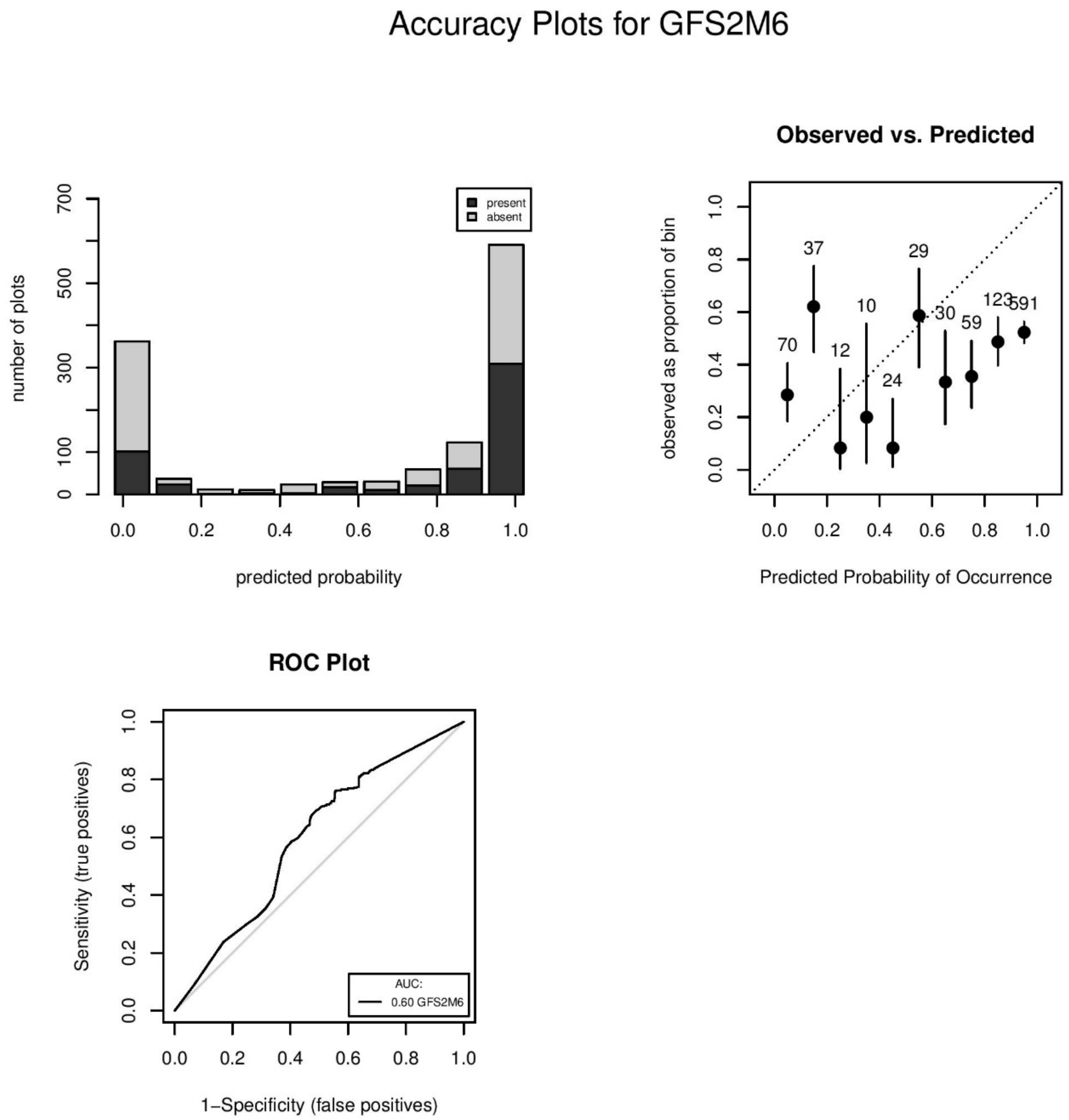

Accuracy Plots for GFS2M2
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
78
21
22
27
16
34
51
68
244
391
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M2


Accuracy Plots for GFS2M3
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
80
22
10
30
23
14
44
68
214
467
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M3

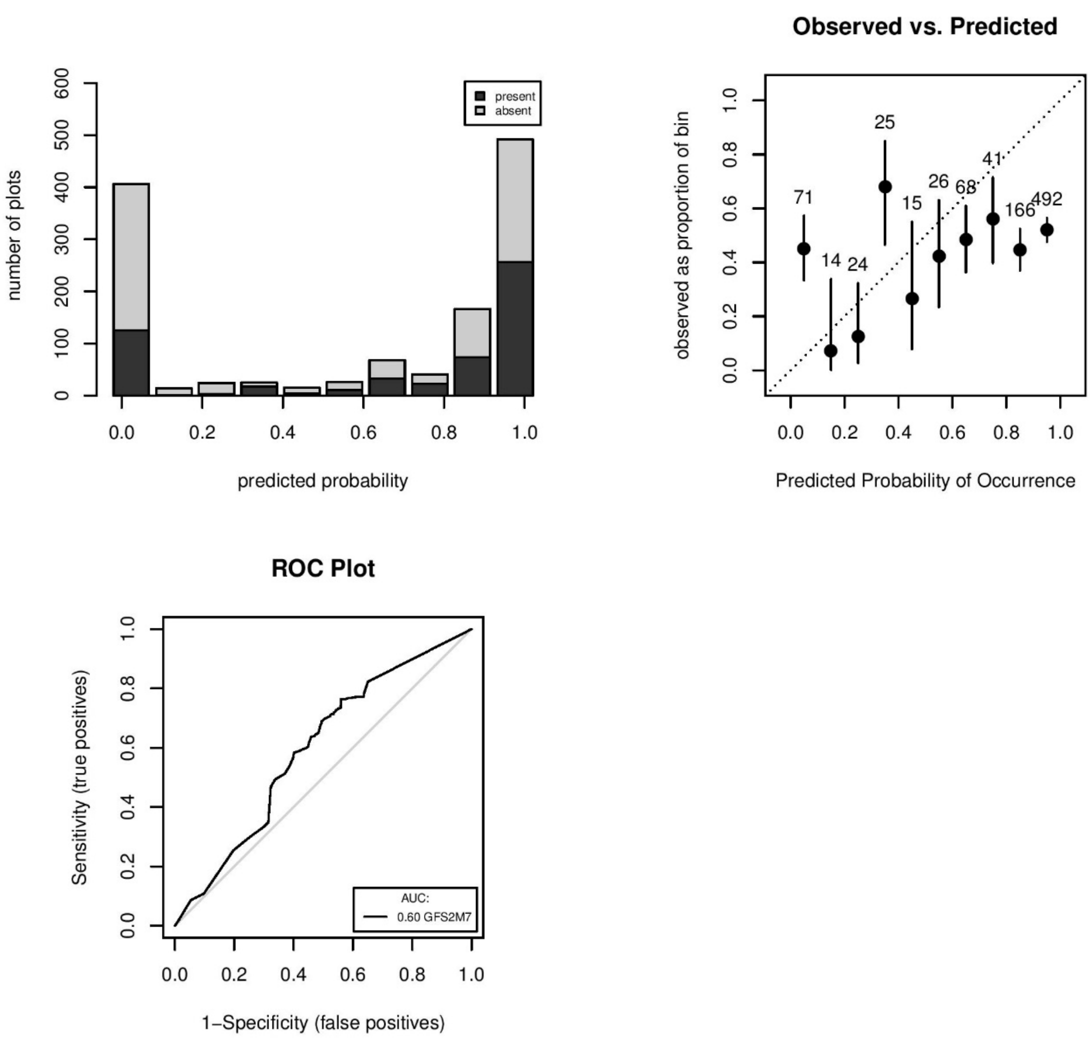

Accuracy Plots for GFS2M4
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
65
23
31
15
23
51
38
62
225
397
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M4

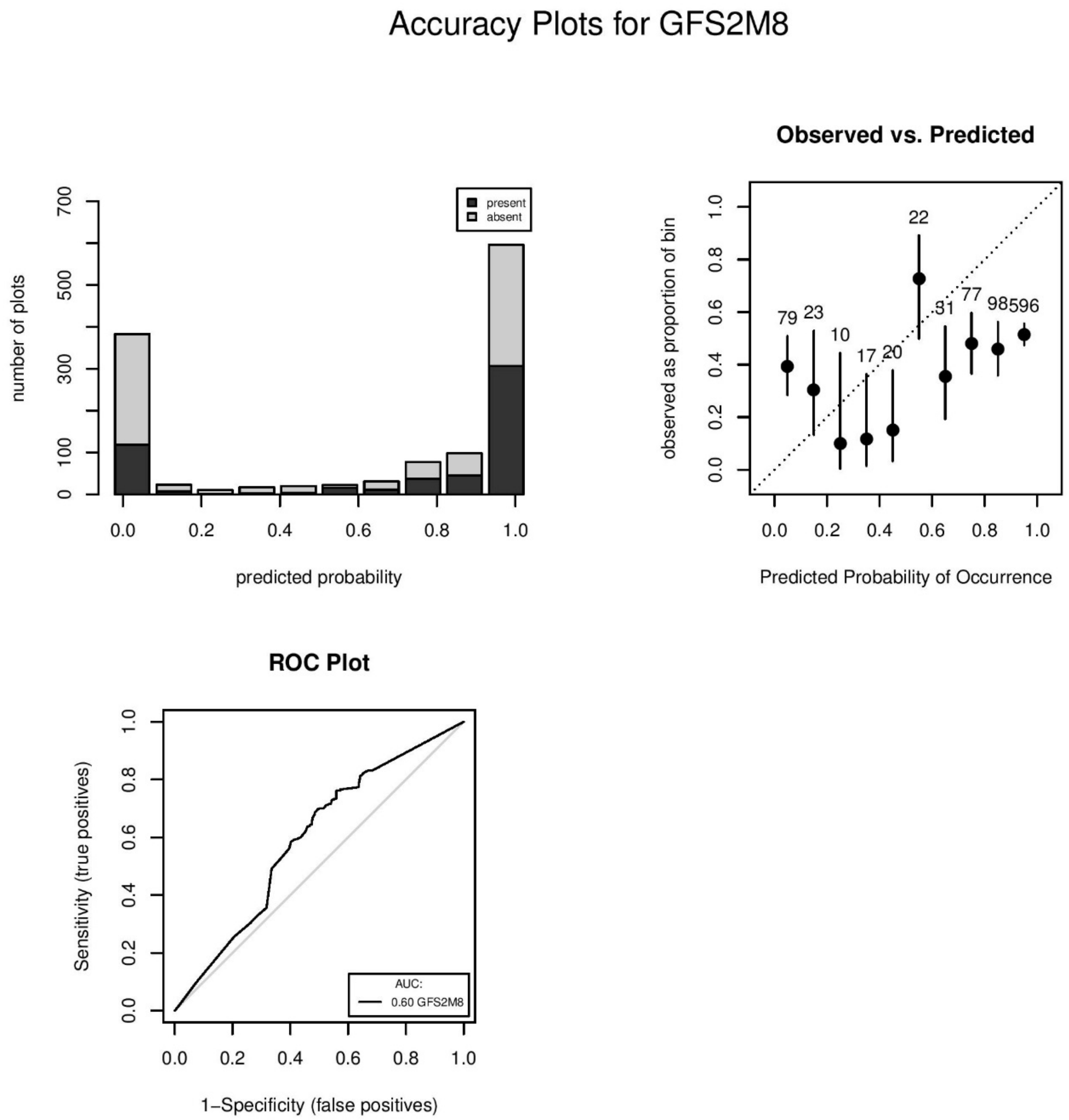
Accuracy Plots for GFS2M5

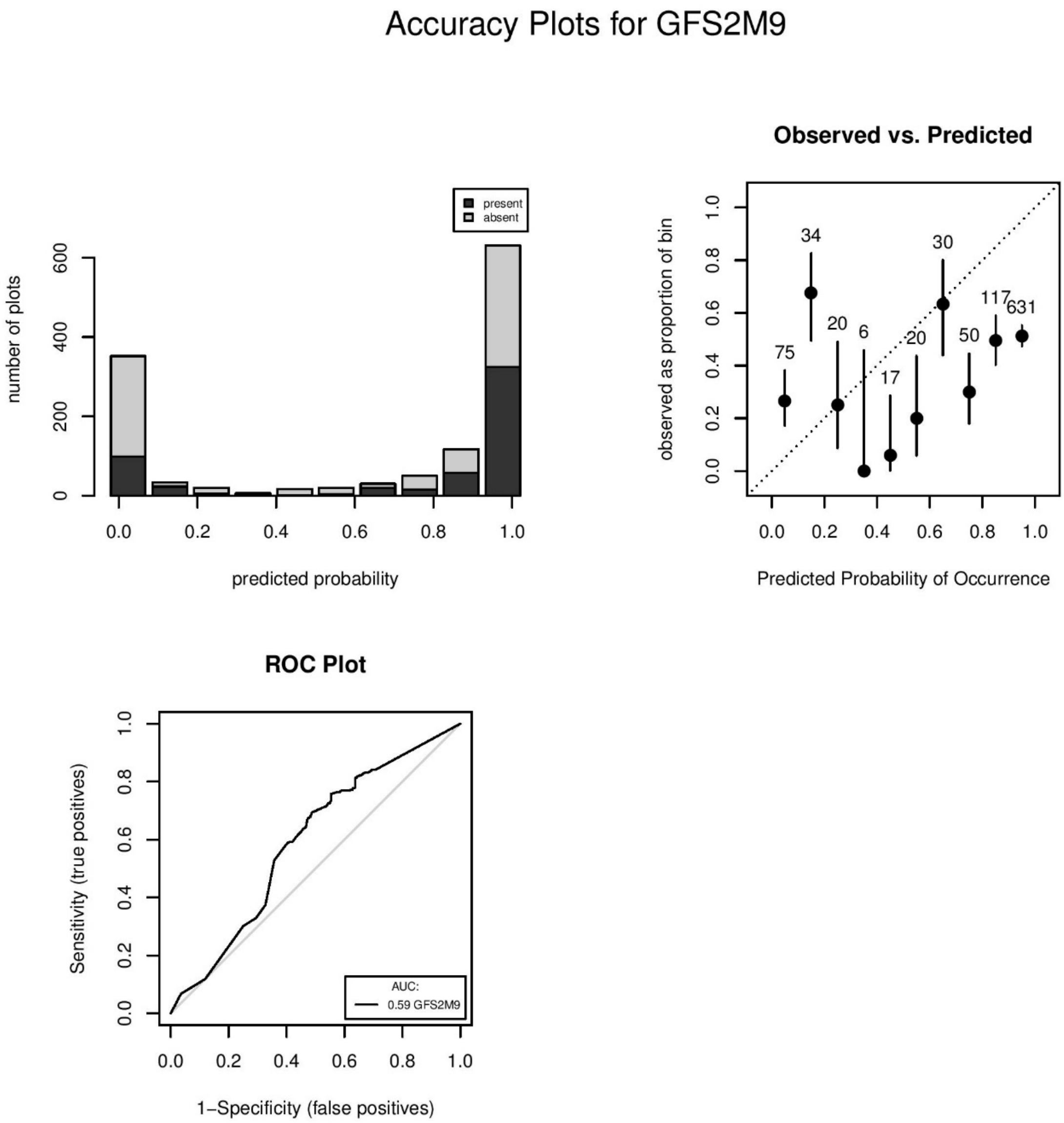


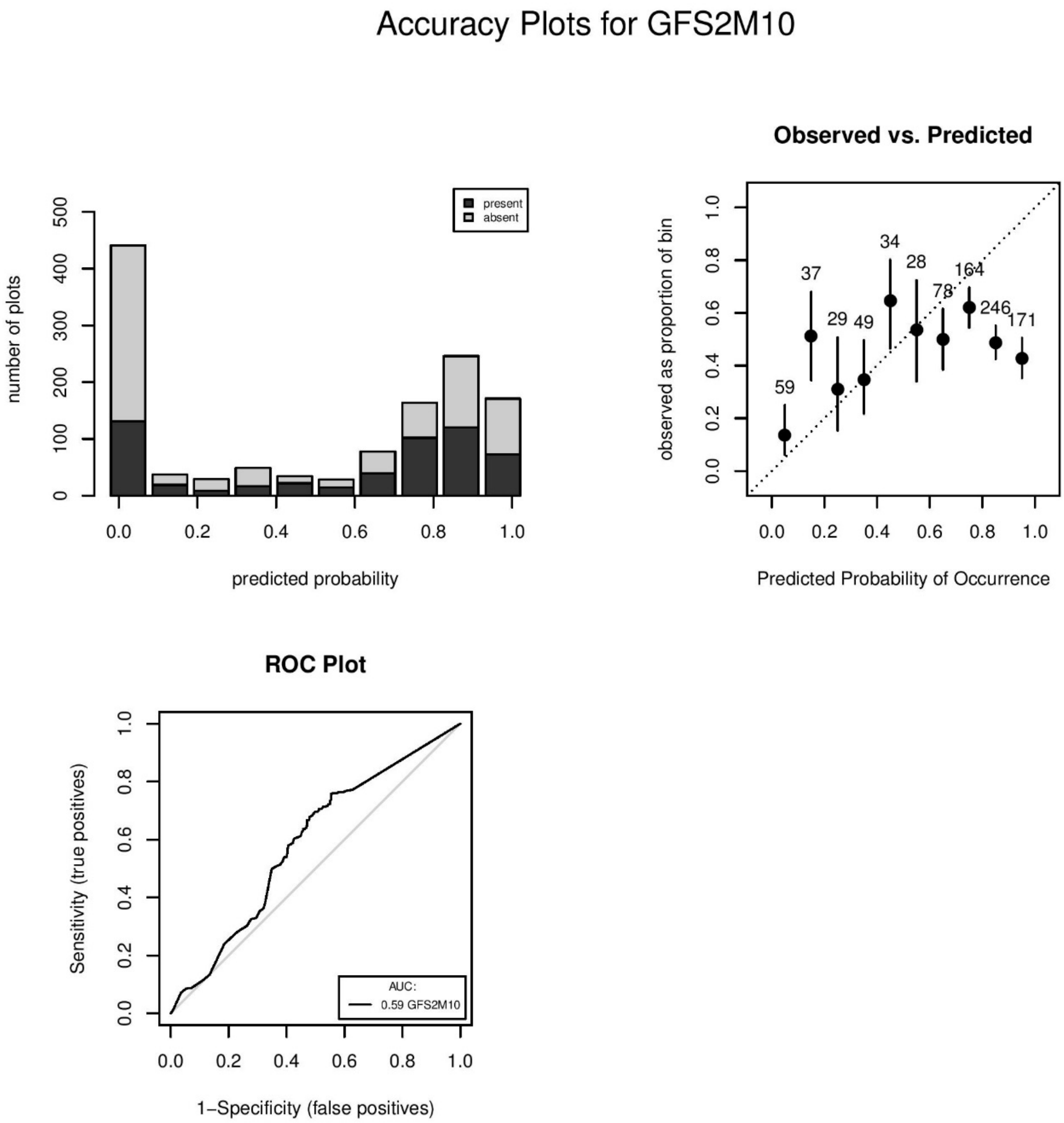

Accuracy Plots for GFS2M6
number of plots
0
100
300
500
700
present
absent
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
0.0
0.2
0.4
0.6
0.8
1.0
70
37
12
10
24
29
30
59
123
591
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.60 GFS2M6
1−Specificity (false positives)

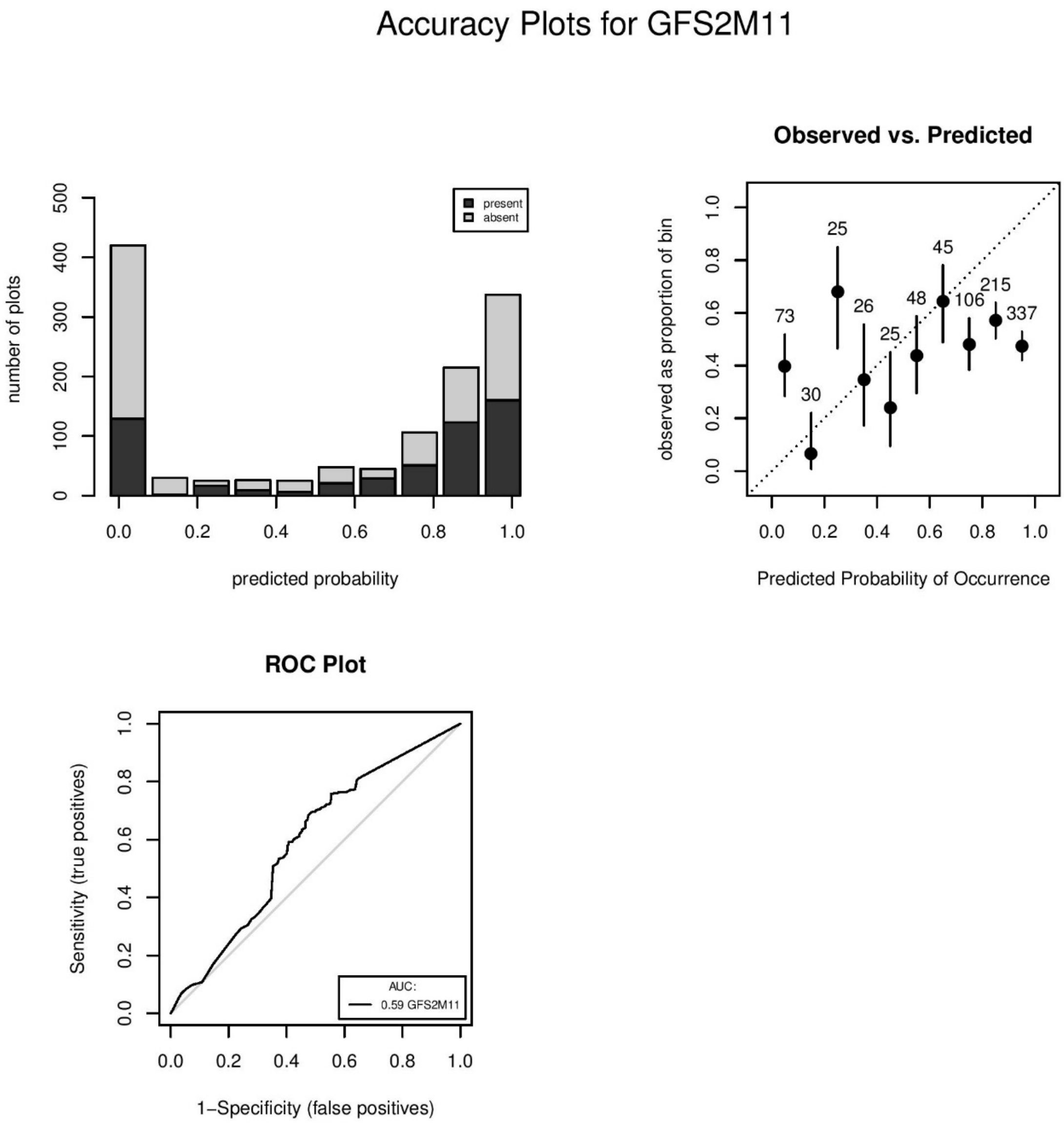
Accuracy Plots for GFS2M7

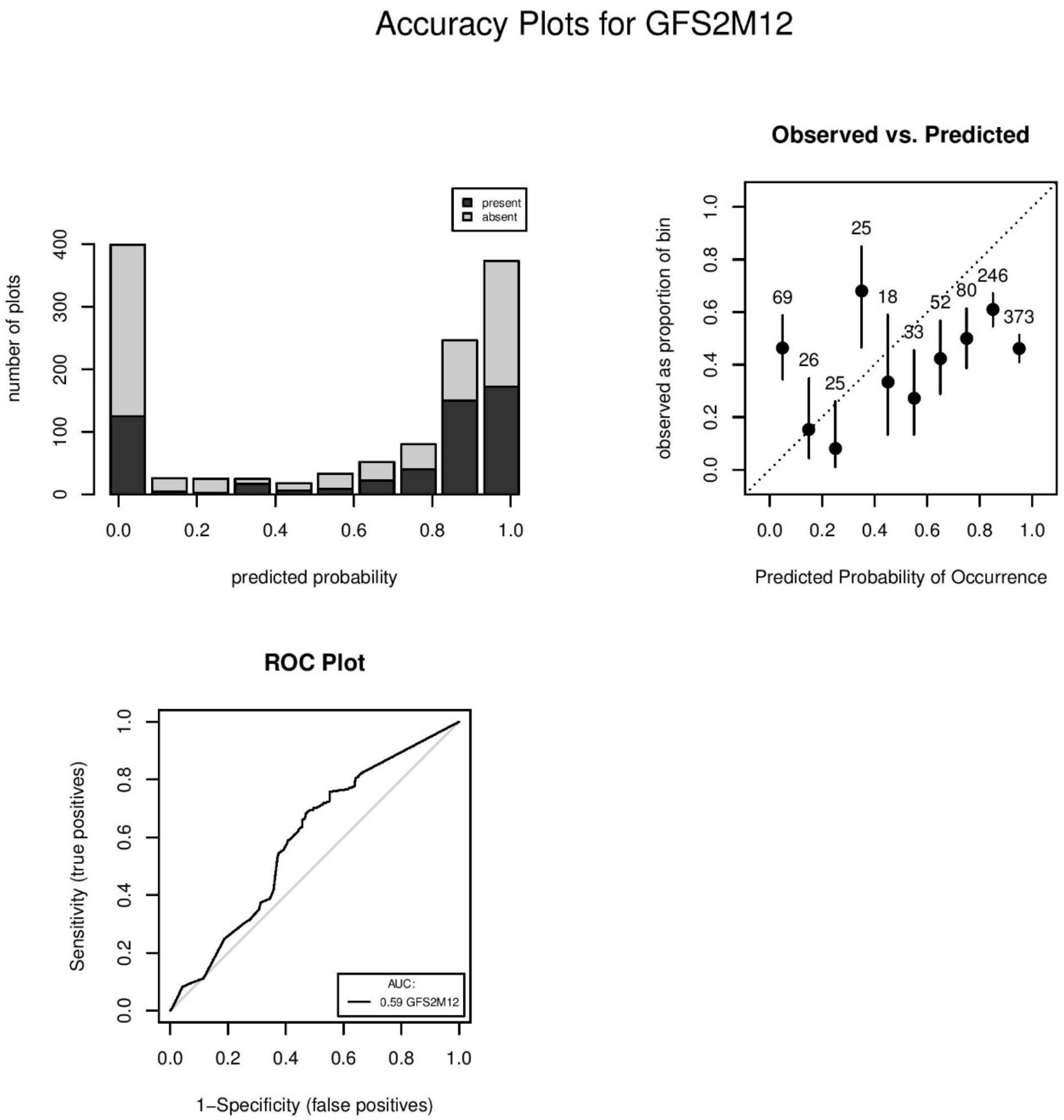


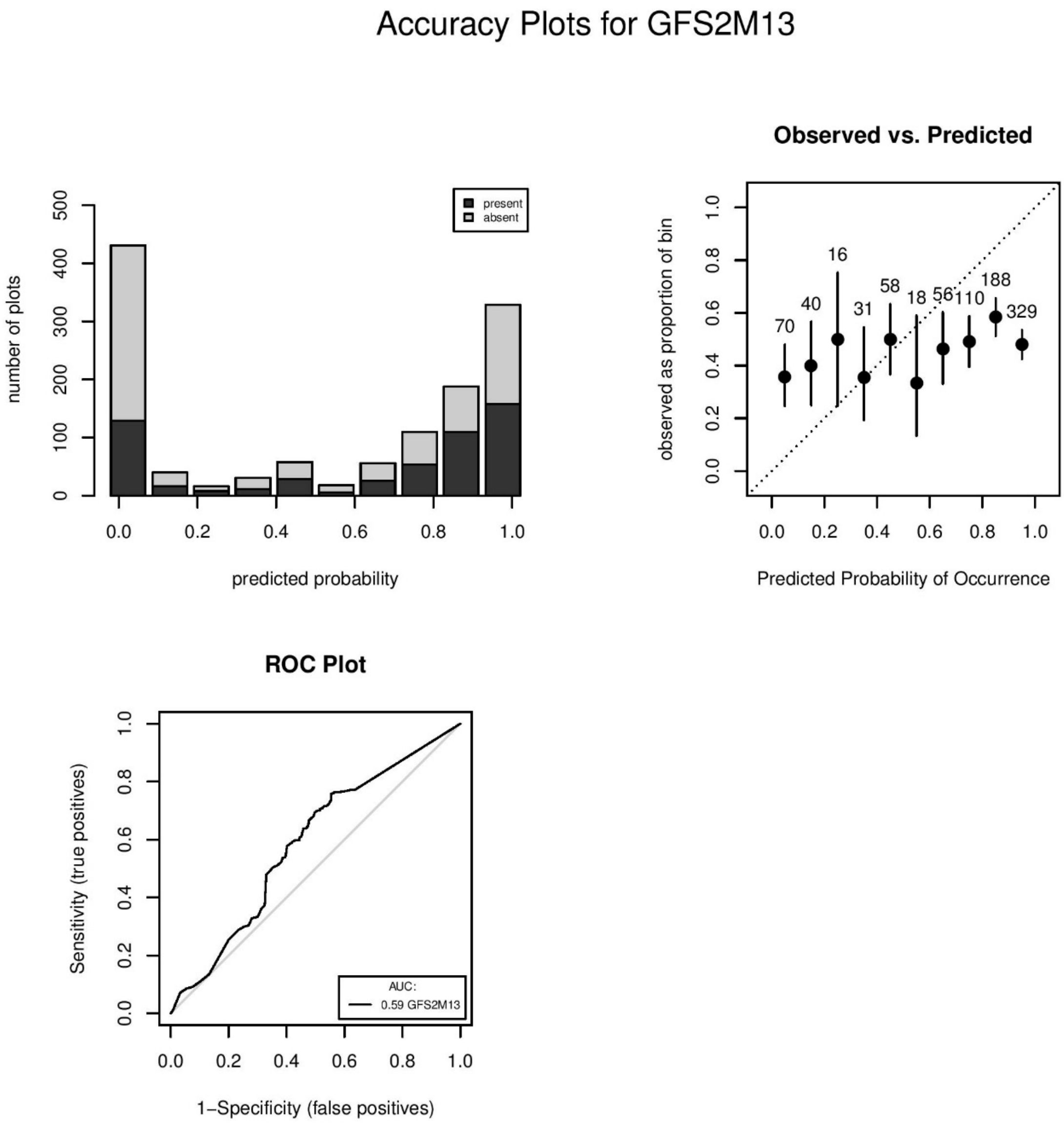

Accuracy Plots for GFS2M8
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
79
23
10
17
20
22
31
77
98
596
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M8

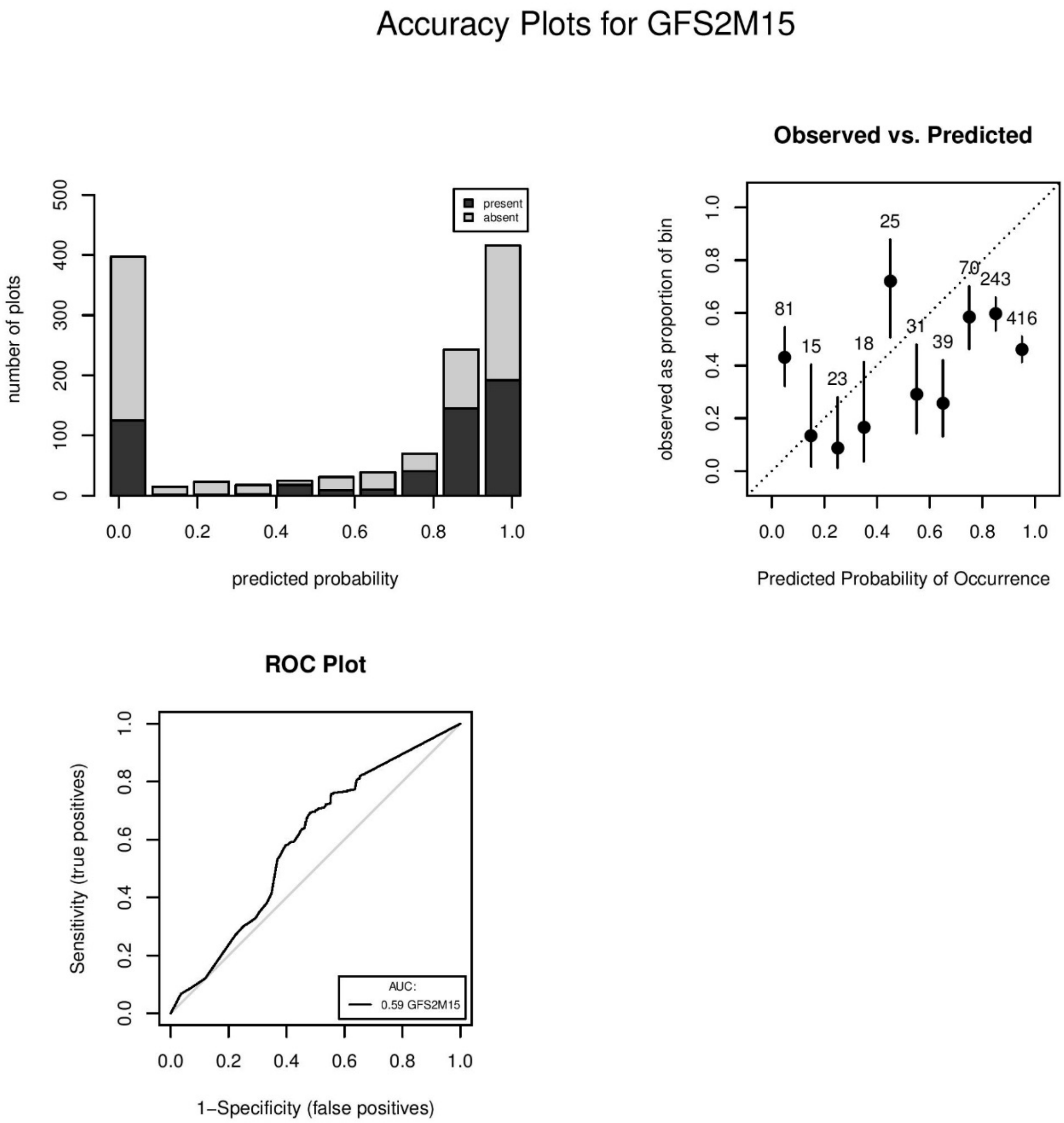

Accuracy Plots for GFS2M9
present
absent
number of plots
0
200
400
600
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
0.0
0.2
0.4
0.6
0.8
1.0
75
34
20
6
17
20
30
50
117
631
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M9

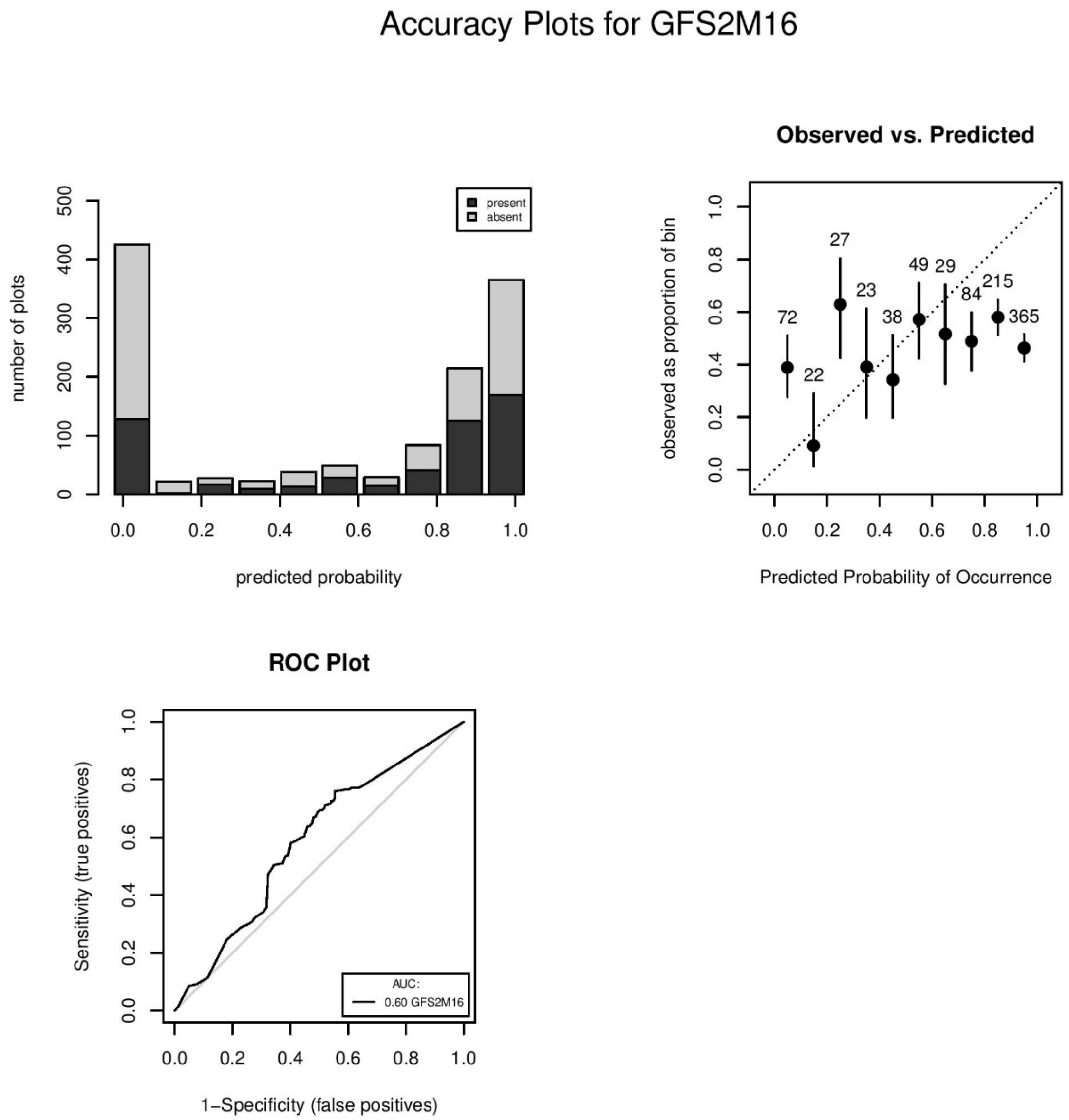

Accuracy Plots for GFS2M10
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
59
37
29
49
34
28
78
164
246
171
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M10


Accuracy Plots for GFS2M11
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
73
30
25
26
25
48
45
106
215
337
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M11

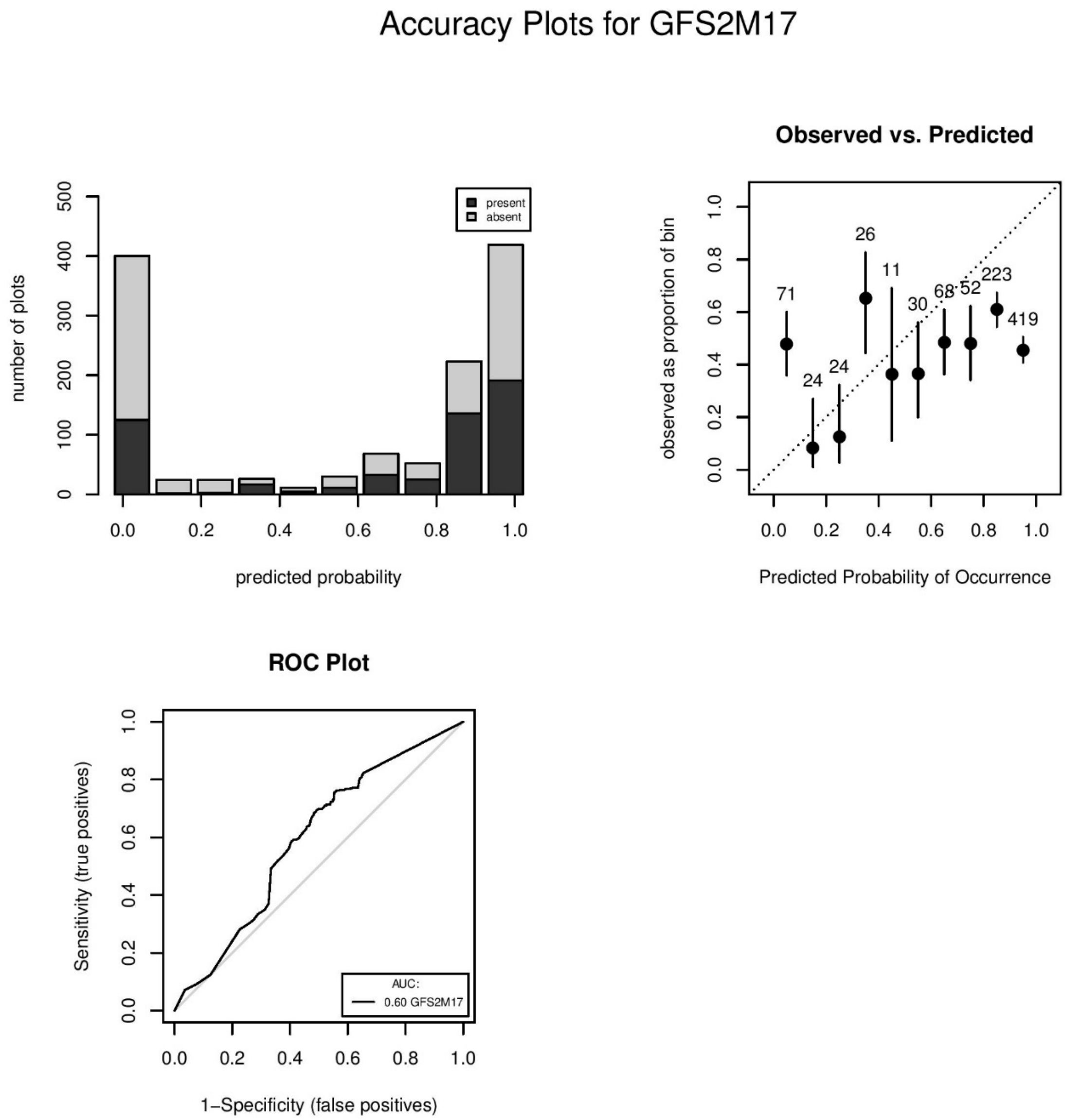

Accuracy Plots for GFS2M12
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
69
26
25
25
18
33
52
80
246
373
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M12


Accuracy Plots for GFS2M13
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
70
40
16
31
58
18
56
110
188
329
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M13

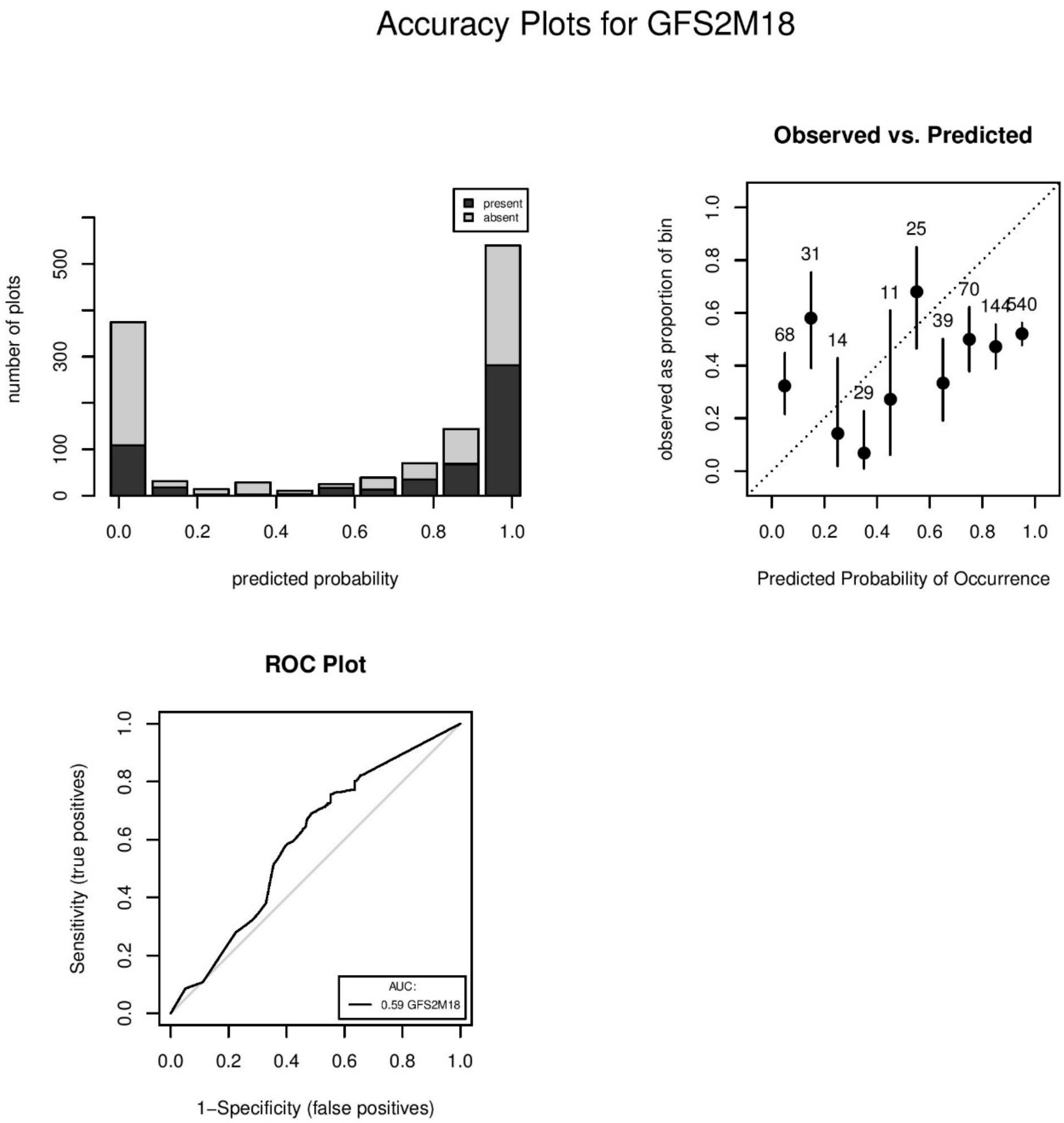

Accuracy Plots for GFS2M15
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
81
15
23
18
25
31
39
70
243
416
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M15

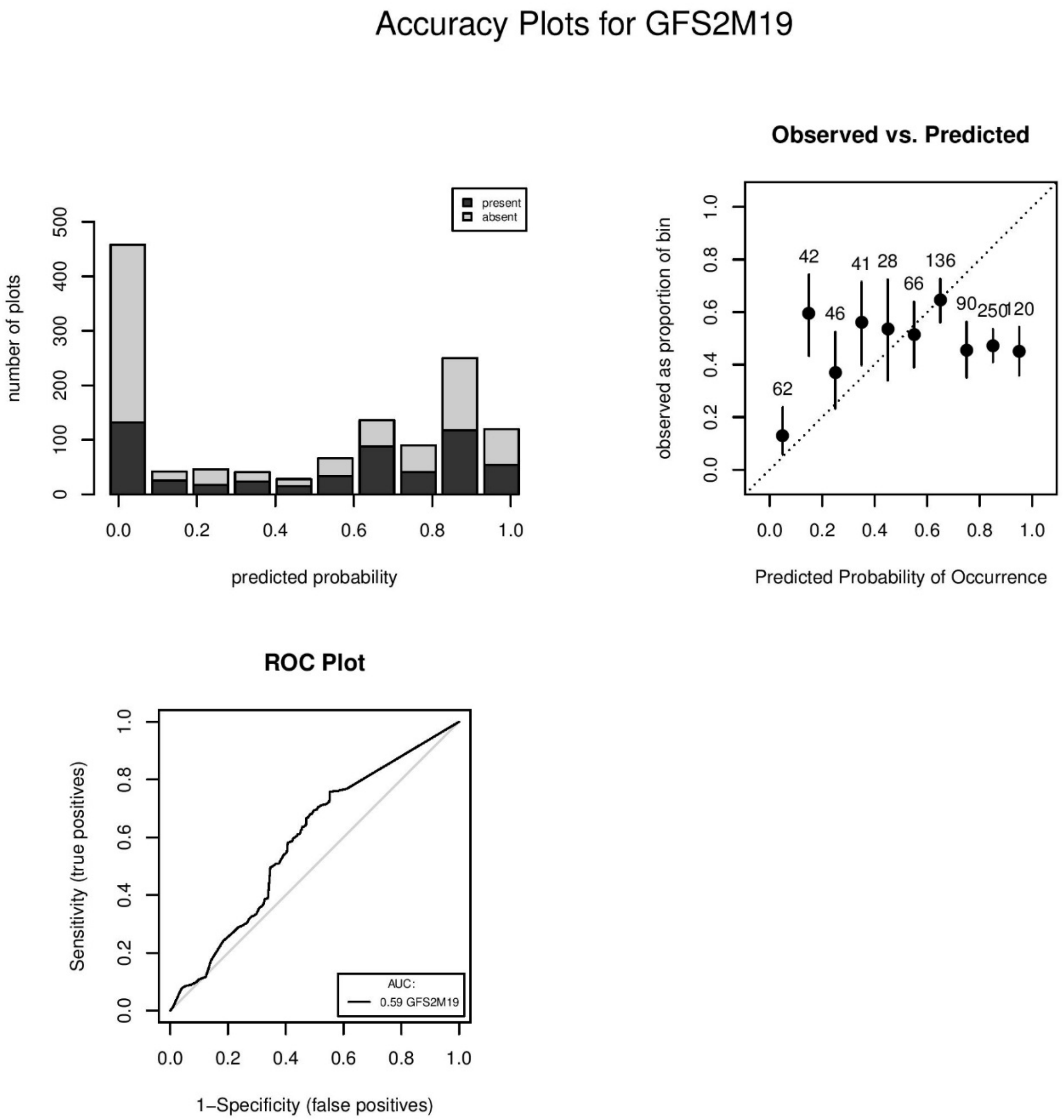


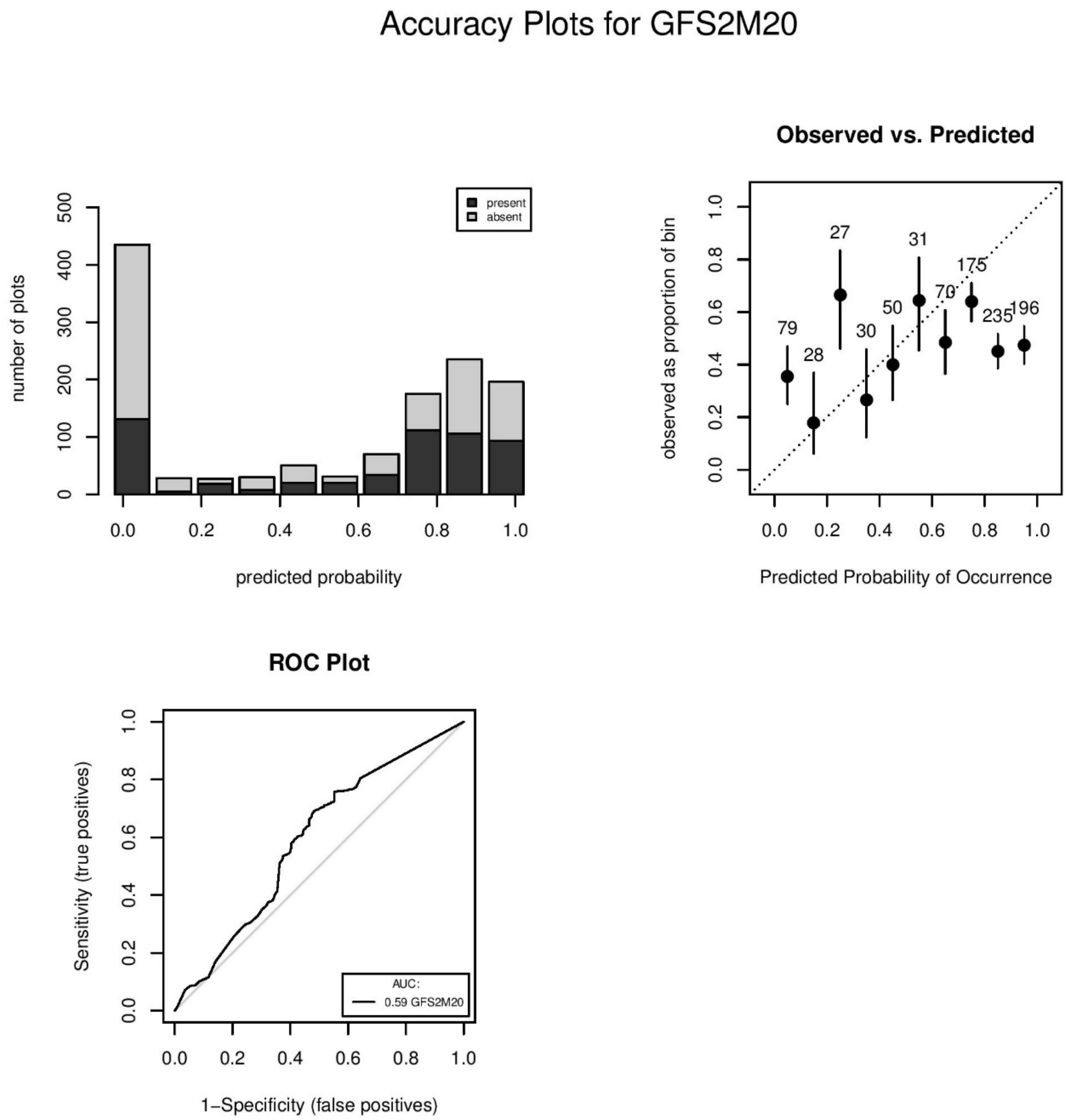
Accuracy Plots for GFS2M16
number of plots
present
absent
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
72
22
27
23
38
49
29
84
215
365
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M16

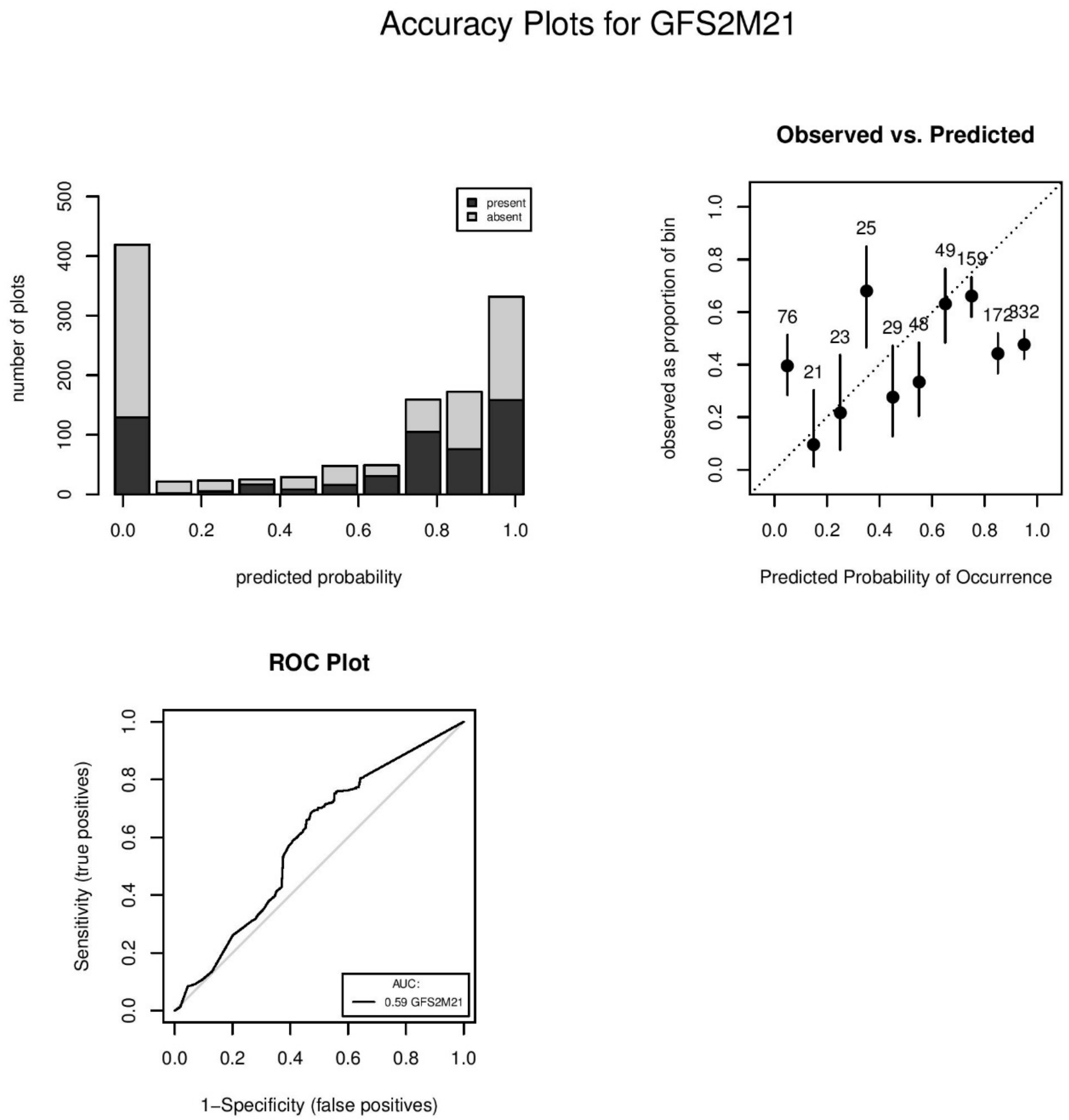


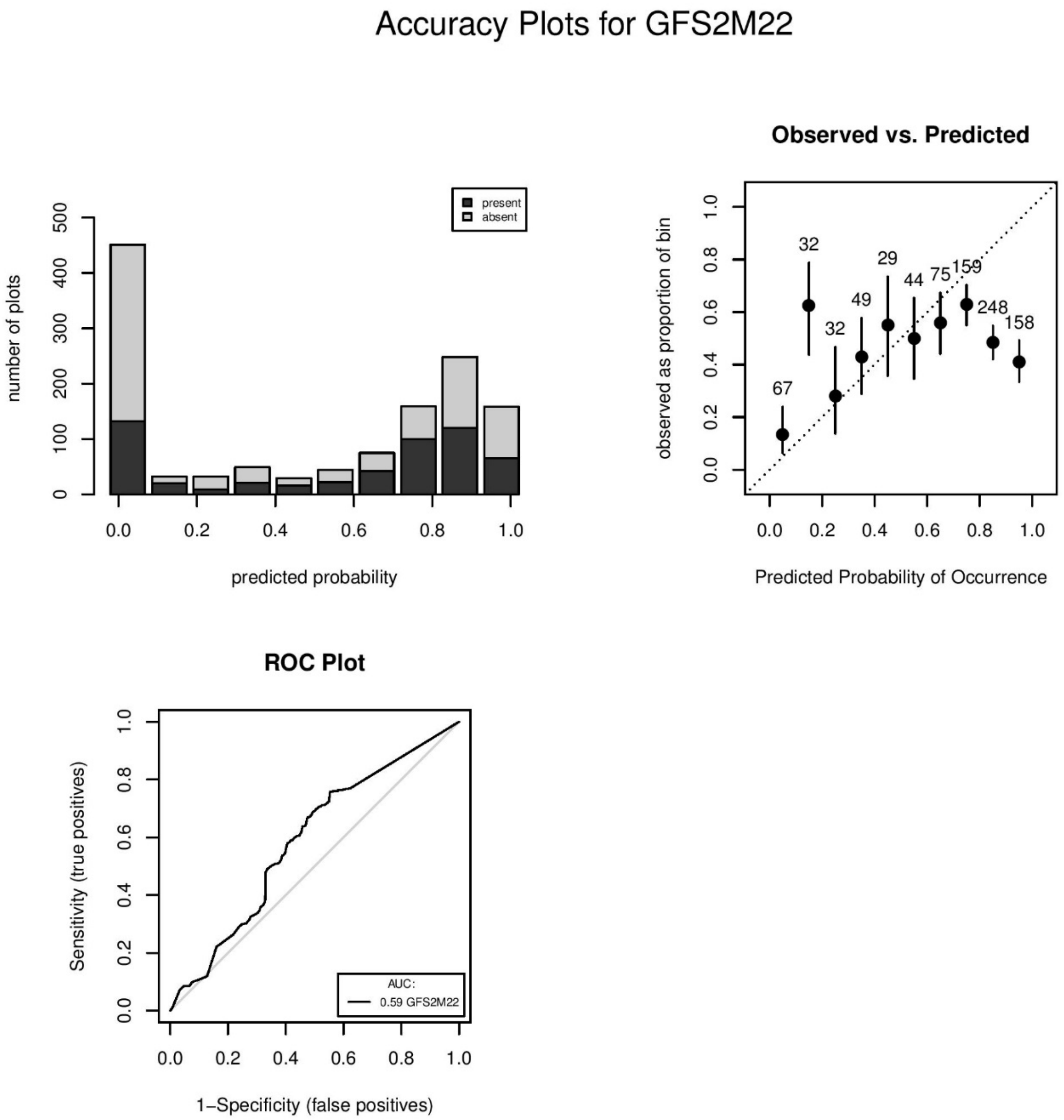
Accuracy Plots for GFS2M17
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
71
24
24
26
11
30
68
52
223
419
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M17


Accuracy Plots for GFS2M18
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
68
31
14
29
11
25
39
70
144
540
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M18

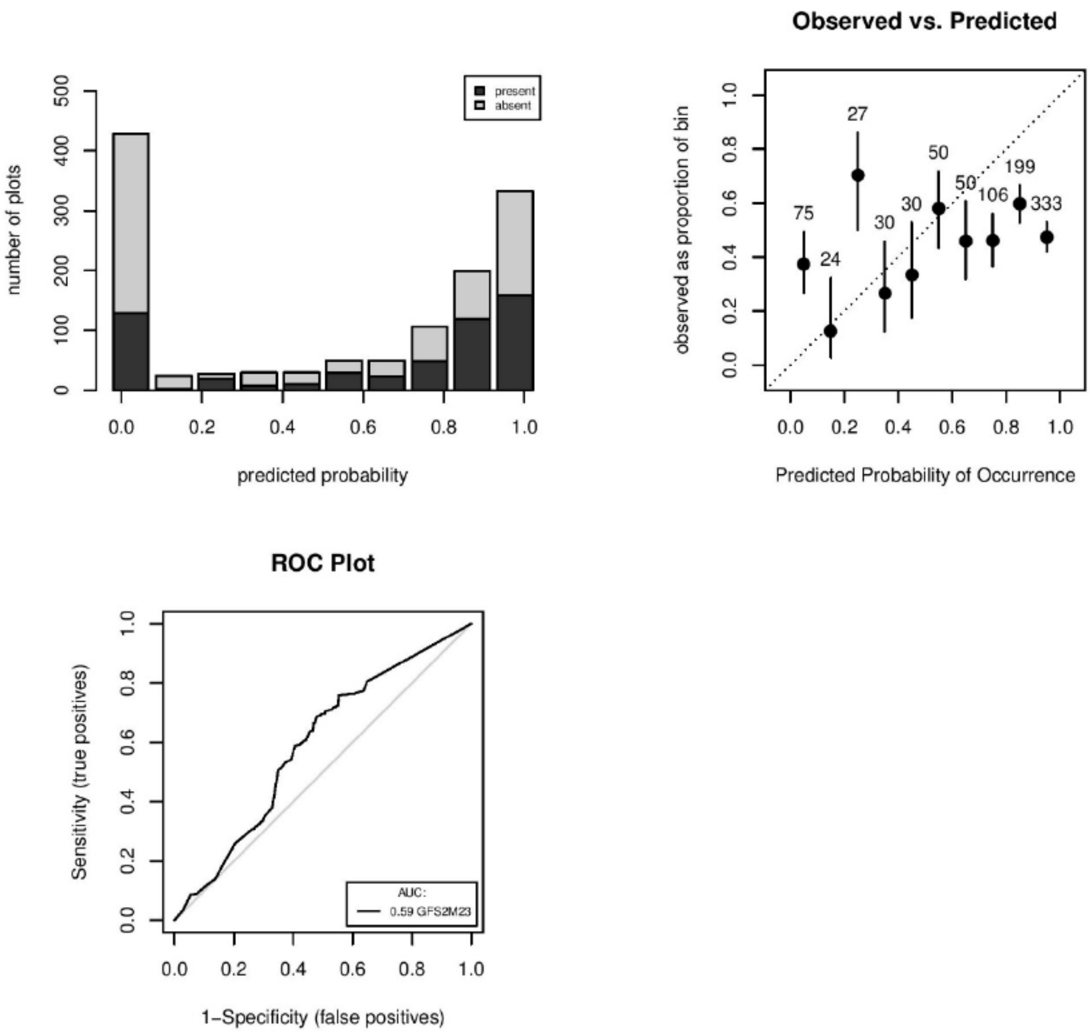

Accuracy Plots for GFS2M19
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
62
42
46
41
28
66
136
90
250
120
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M19

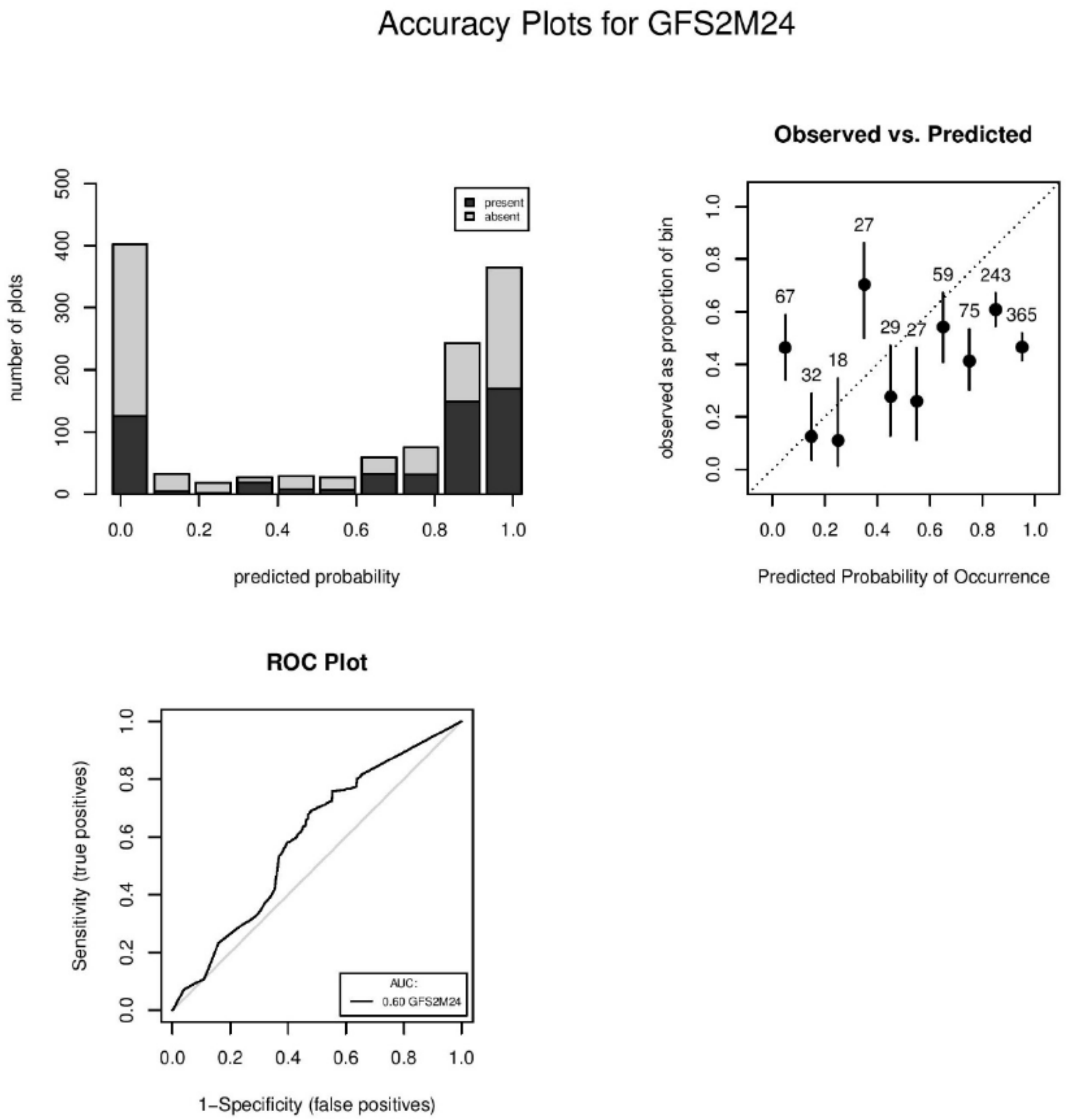

Accuracy Plots for GFS2M20
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
79
28
27
30
50
31
70
175
235
196
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M20

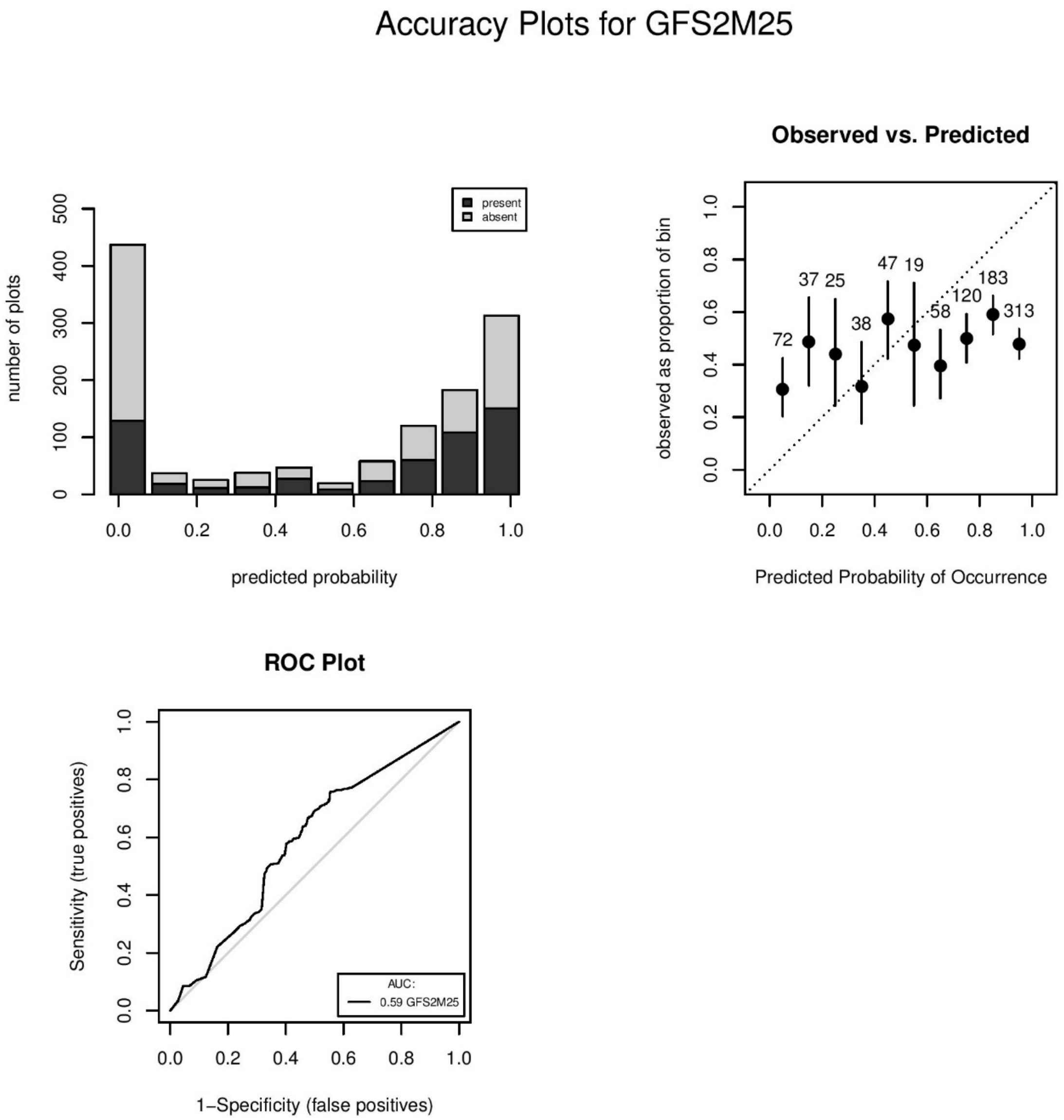

Accuracy Plots for GFS2M21
number of plots
predicted probability
present
absent
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
76
21
23
25
29
48
49
159
172
332
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M21

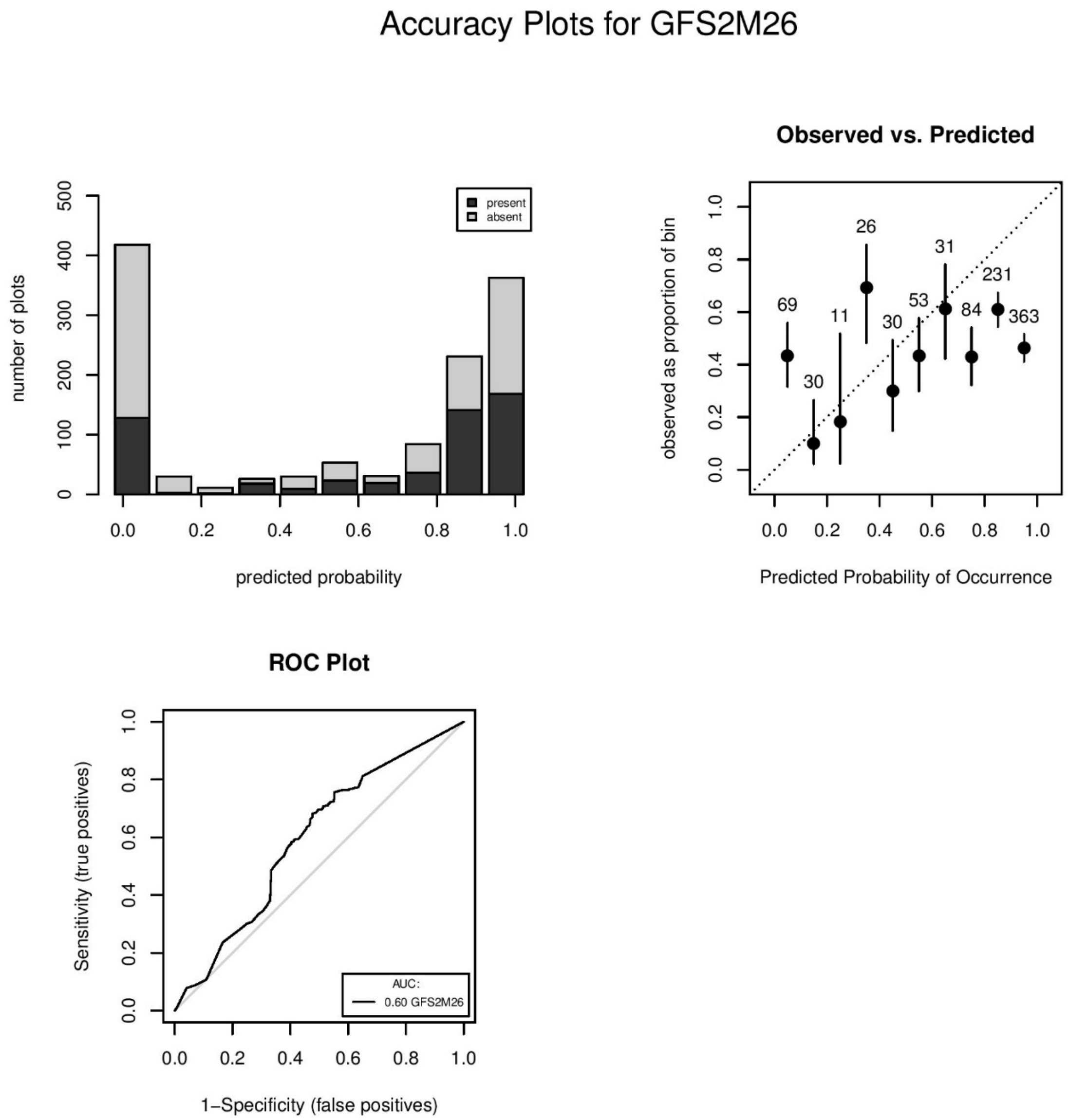

Accuracy Plots for GFS2M22
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
67
32
32
49
29
44
75
159
248
158
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M22

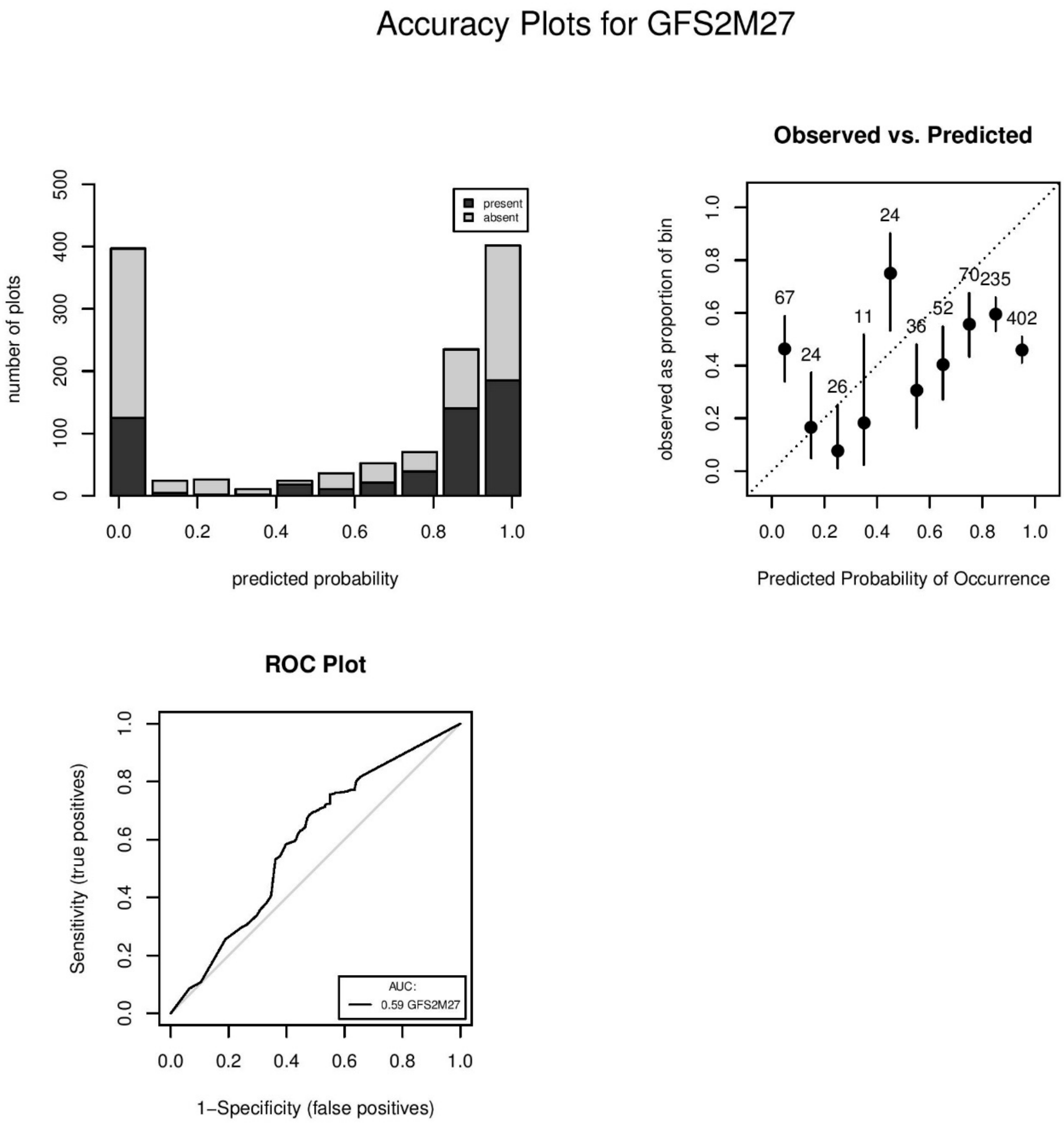
Accuracy Plots for GFS2M23

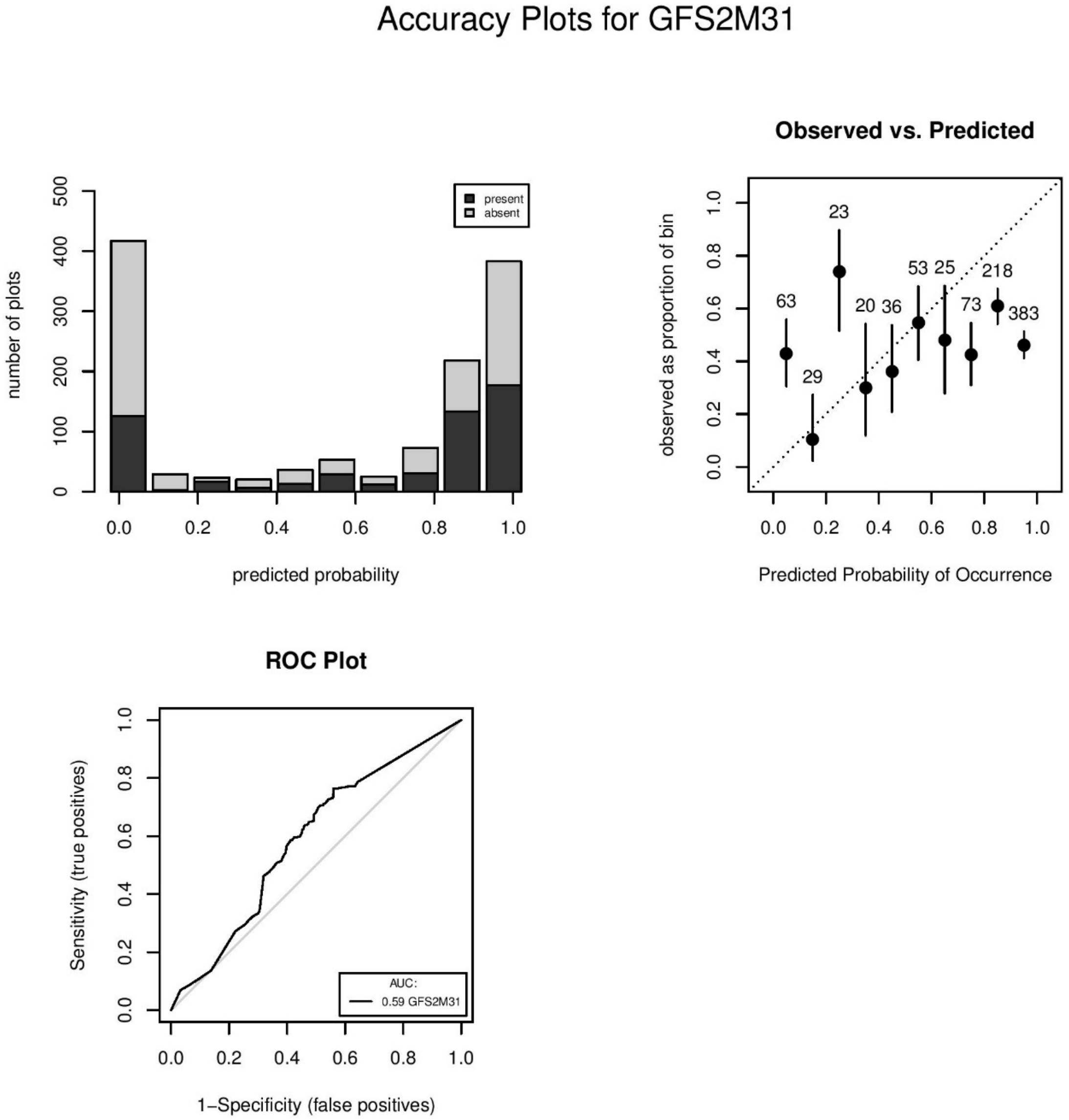


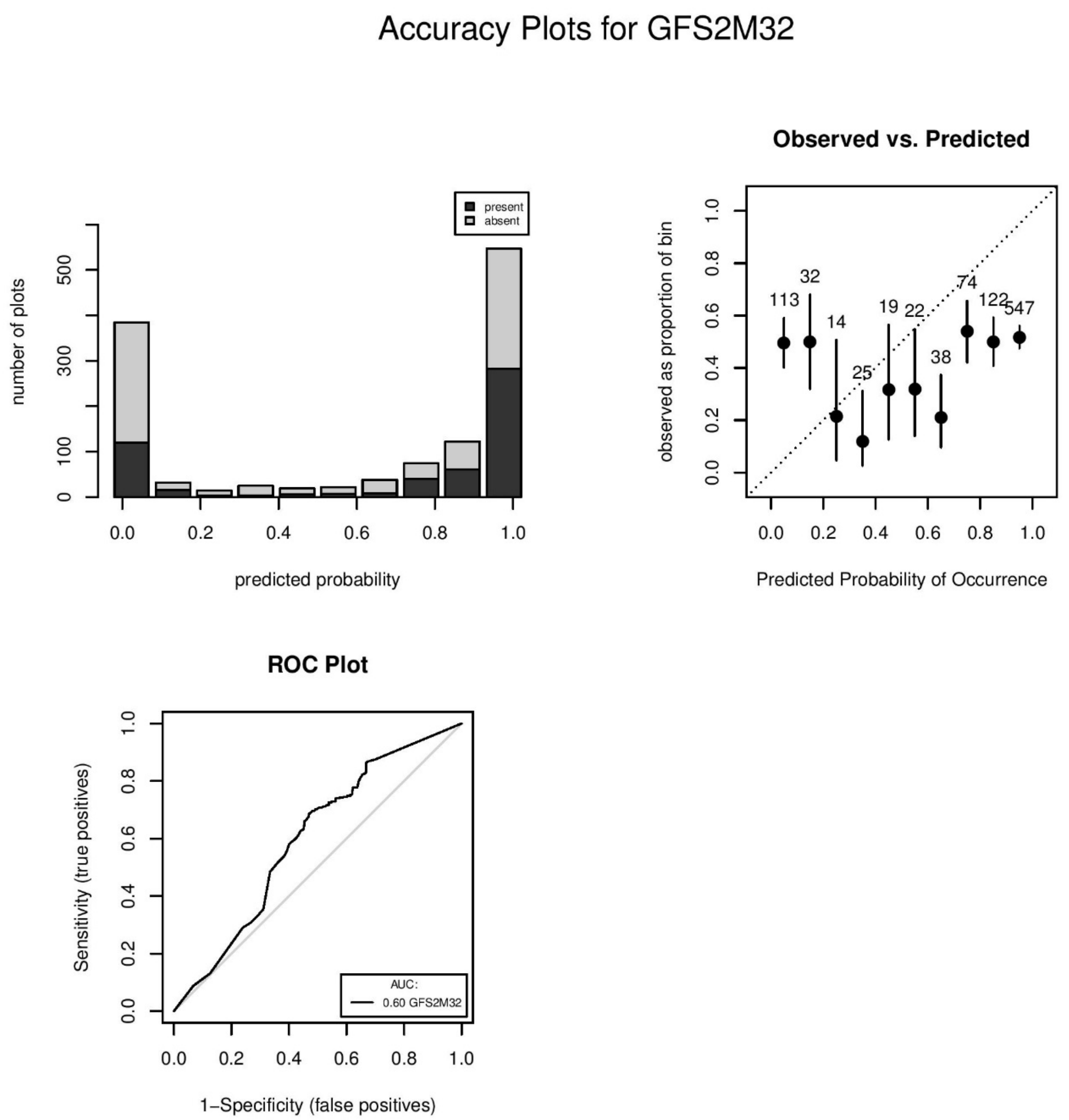

Accuracy Plots for GFS2M24
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
67
32
18
27
29
27
59
75
243
365
ROC Plot
Sensitivity (true positives)
1–Specificity (false positives)
AUC:
0.60 GFS2M24

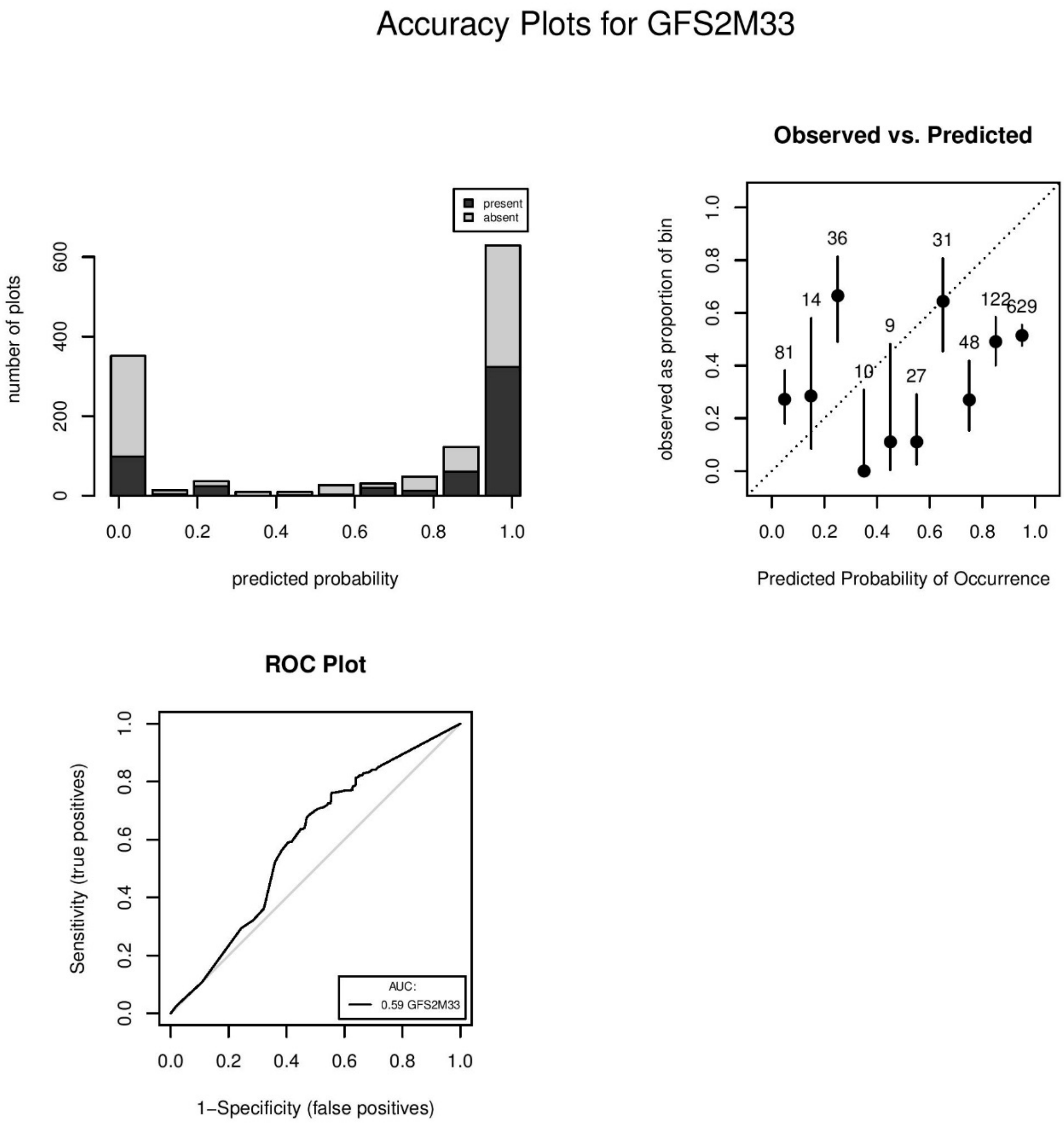

Accuracy Plots for GFS2M25
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
72
37 25
38
47 19
58
120
183
313
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.59 GFS2M25
1−Specificity (false positives)

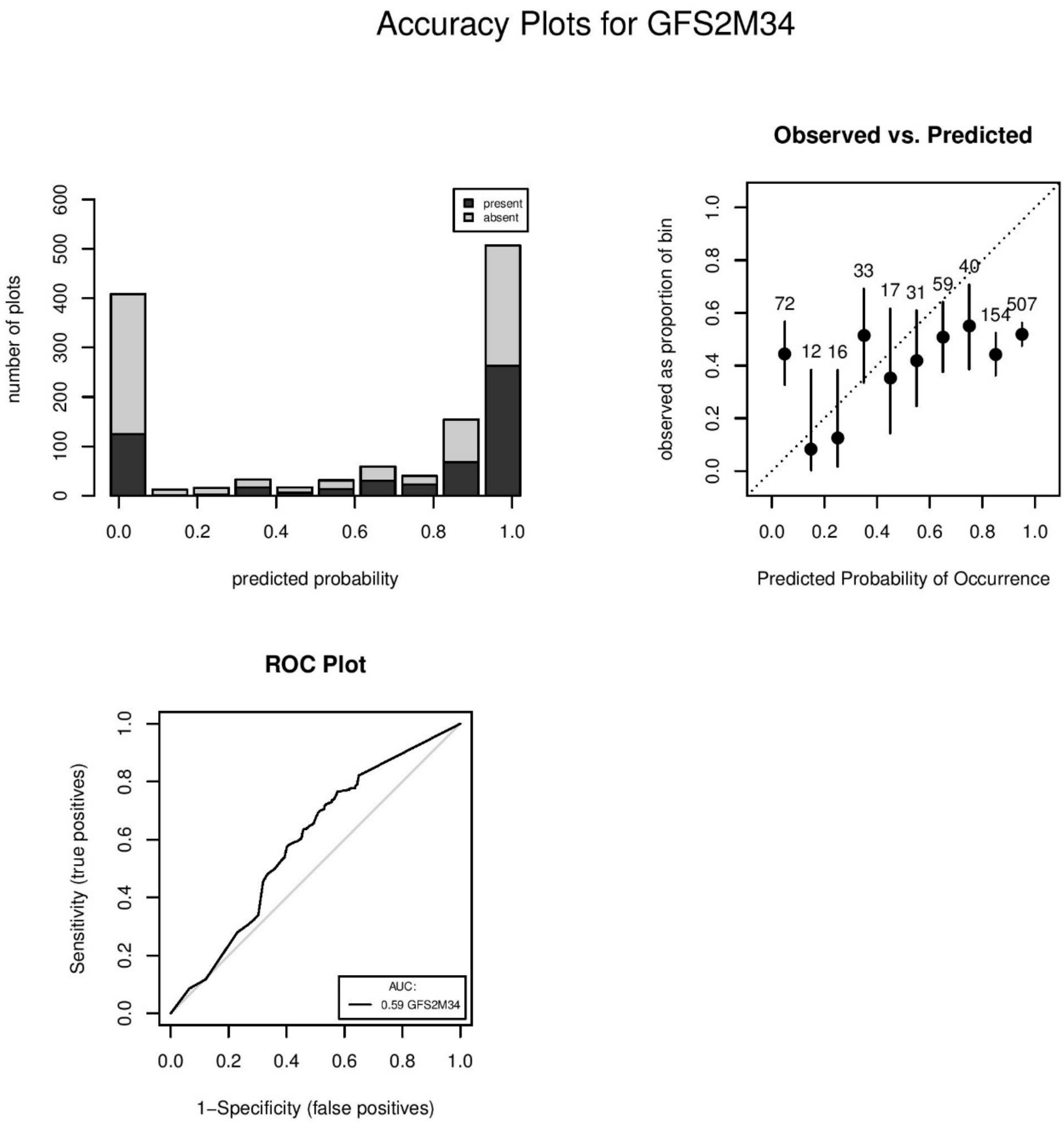

Accuracy Plots for GFS2M26
number of plots
present
absent
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
69
30
11
26
30
53
31
84
231
363
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M26


Accuracy Plots for GFS2M27
number of plots
predicted probability
present
absent
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
67
24
26
11
24
36
52
70
235
402
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M27

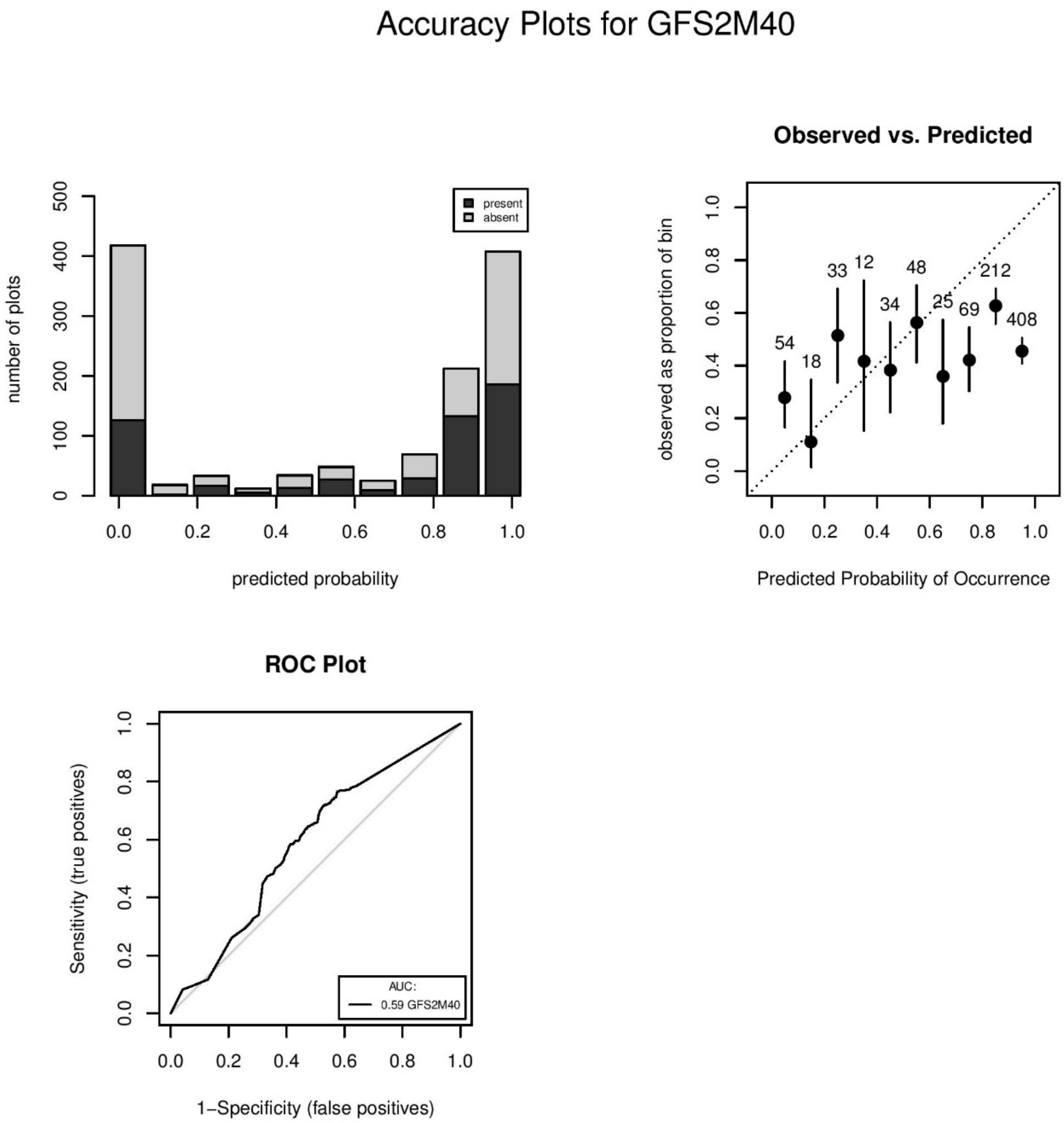

Accuracy Plots for GFS2M31
number of plots
present
absent
predicted probability
Observed vs. Predicted
observed as proportion of bin
63
29
23
20 36
53 25
73
218
383
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.59 GFS2M31
1−Specificity (false positives)

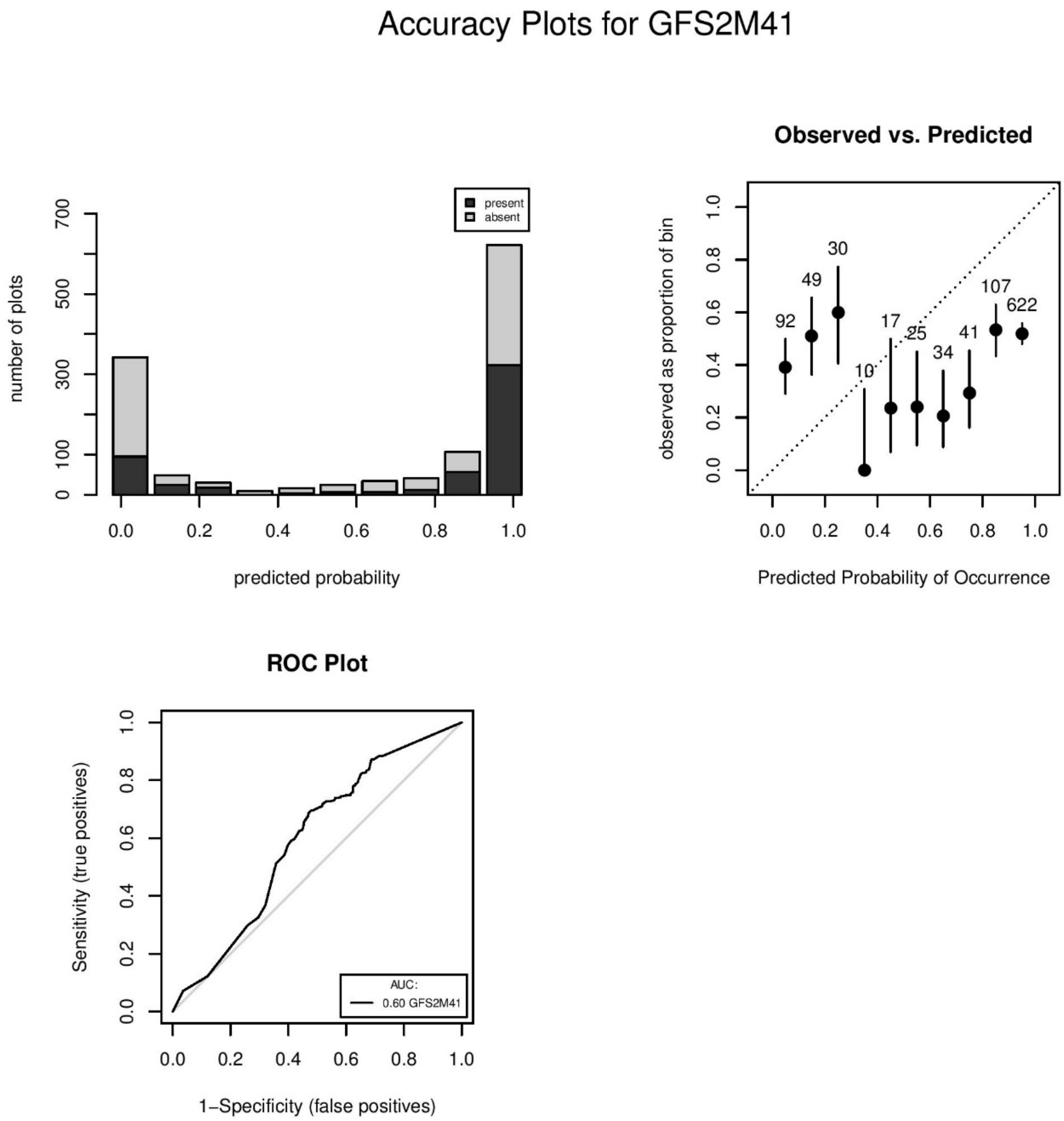

Accuracy Plots for GFS2M32
present
absent
number of plots
0
100
300
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
113
32
14
25
19
22
38
74
122
547
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M32

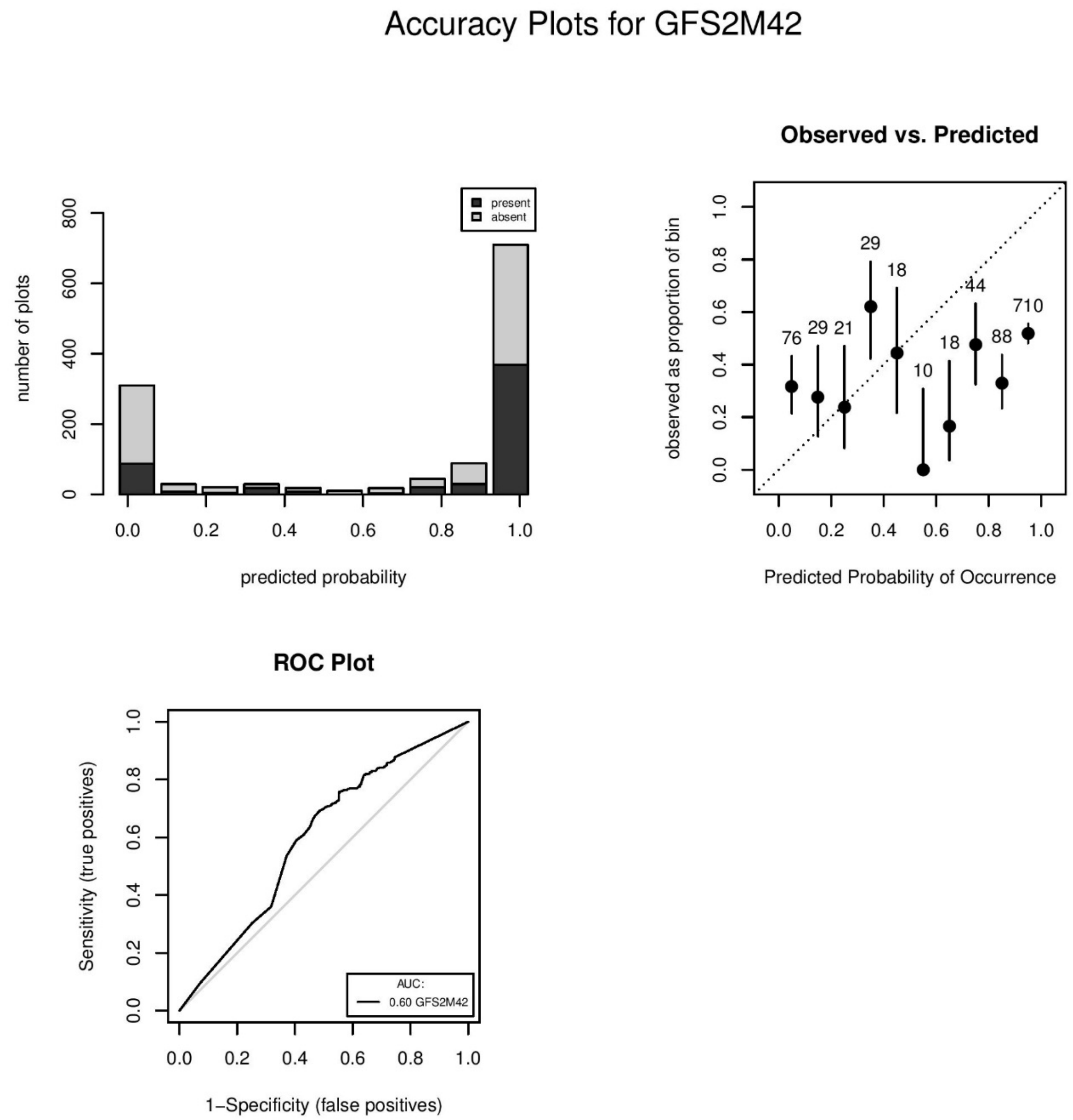

Accuracy Plots for GFS2M33
present
absent
number of plots
0
200
400
600
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
81
14
36
10
9
27
31
48
122
629
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M33

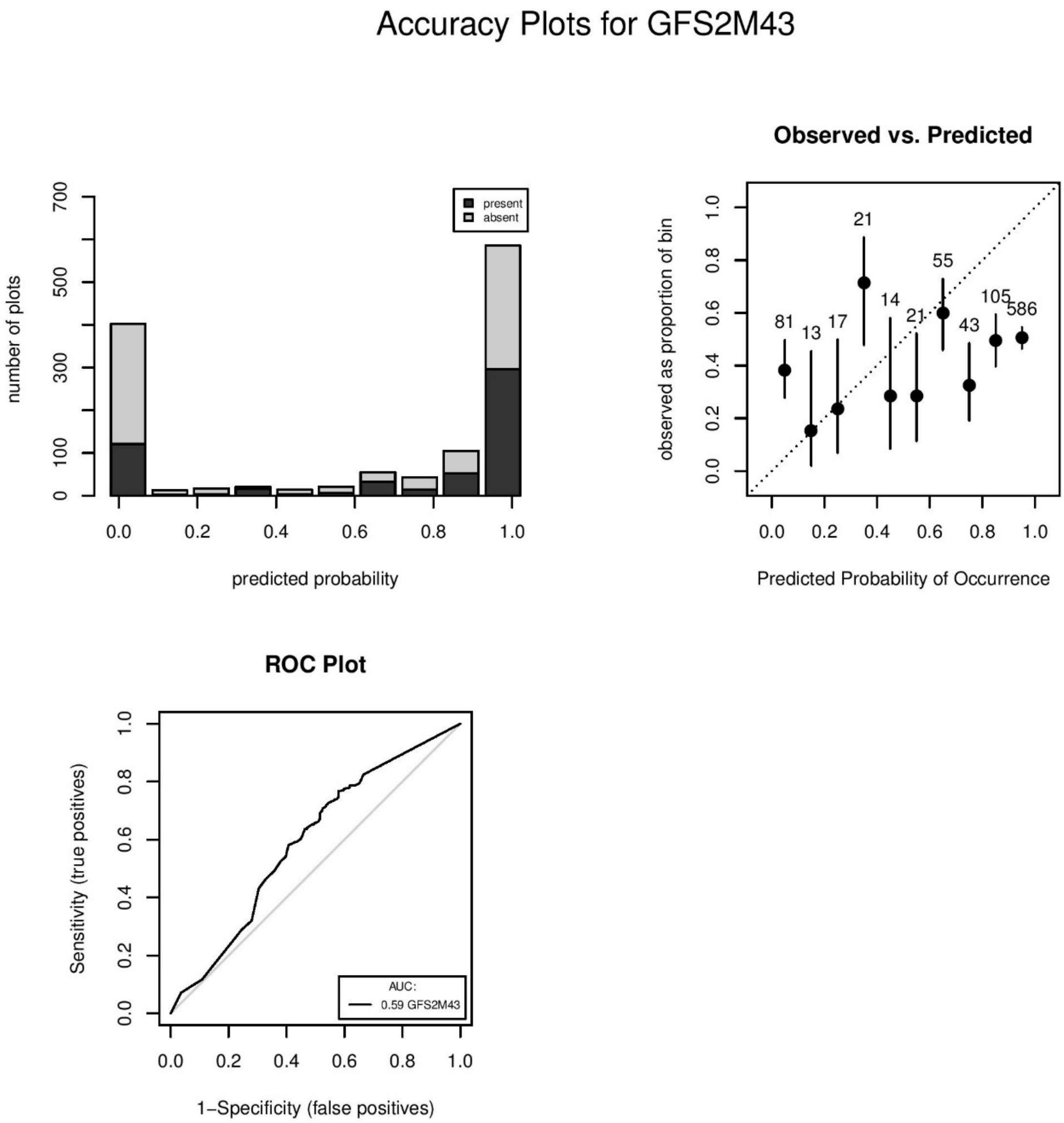


Accuracy Plots for GFS2M34
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
72
12 16
33
17 31
59
40
154
507
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M34

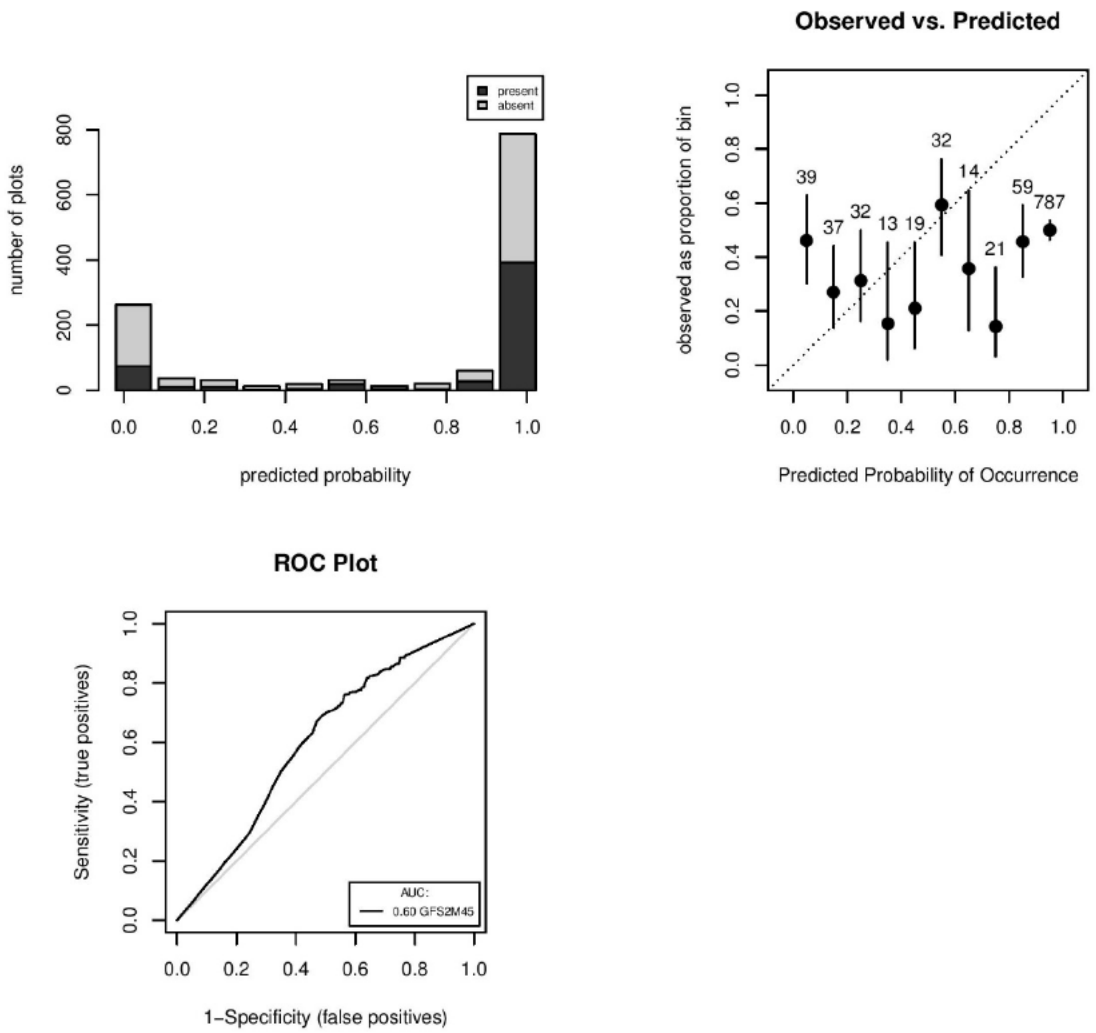

Accuracy Plots for GFS2M40
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
54
18
33
12
34
48
25
69
212
408
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M40


Accuracy Plots for GFS2M41
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
92
49
30
10
17
25
34
41
107
622
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M41

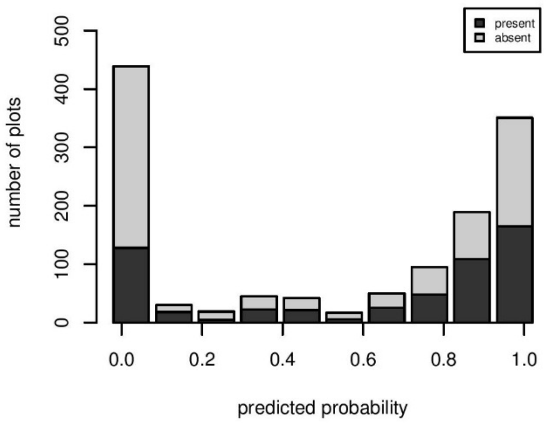

Accuracy Plots for GFS2M42
present
absent
number of plots
0
200
400
600
800
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
76
29
21
29
18
10
18
44
88
710
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.60 GFS2M42
1−Specificity (false positives)

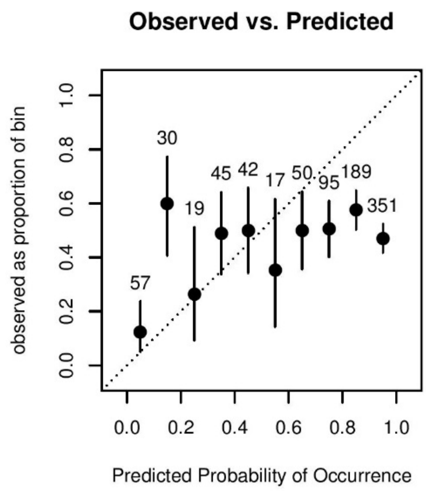

Accuracy Plots for GFS2M43
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
81
13
17
21
14
21
55
43
105
586
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M43

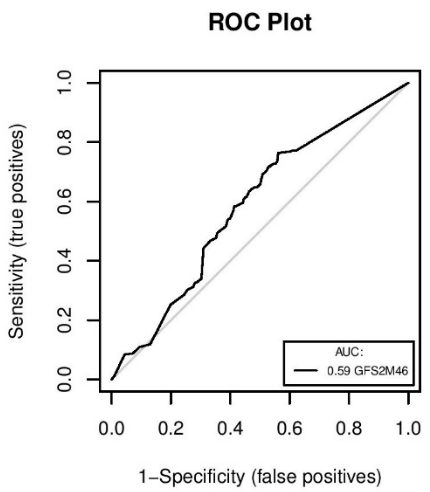
Accuracy Plots for GFS2M45

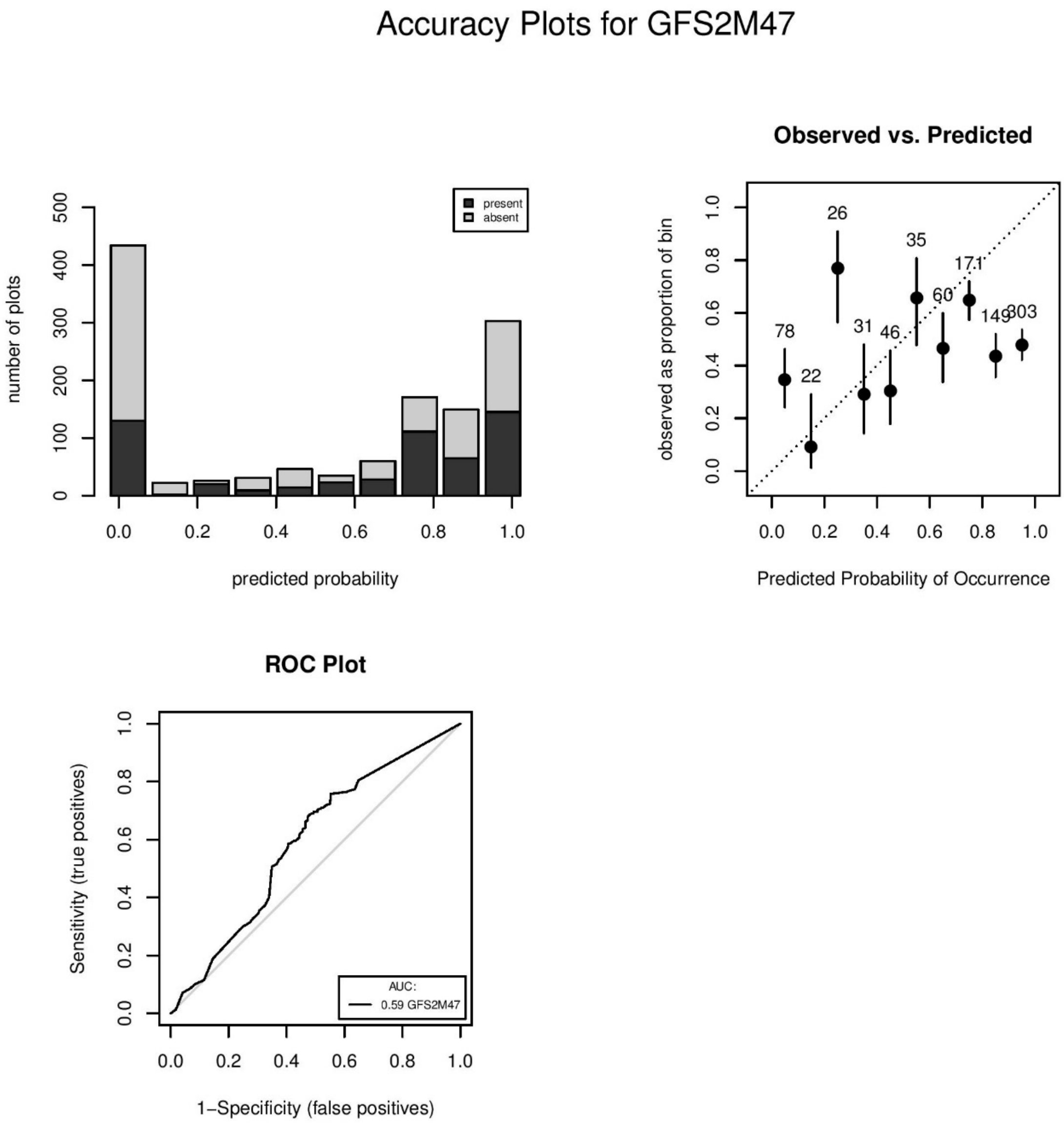


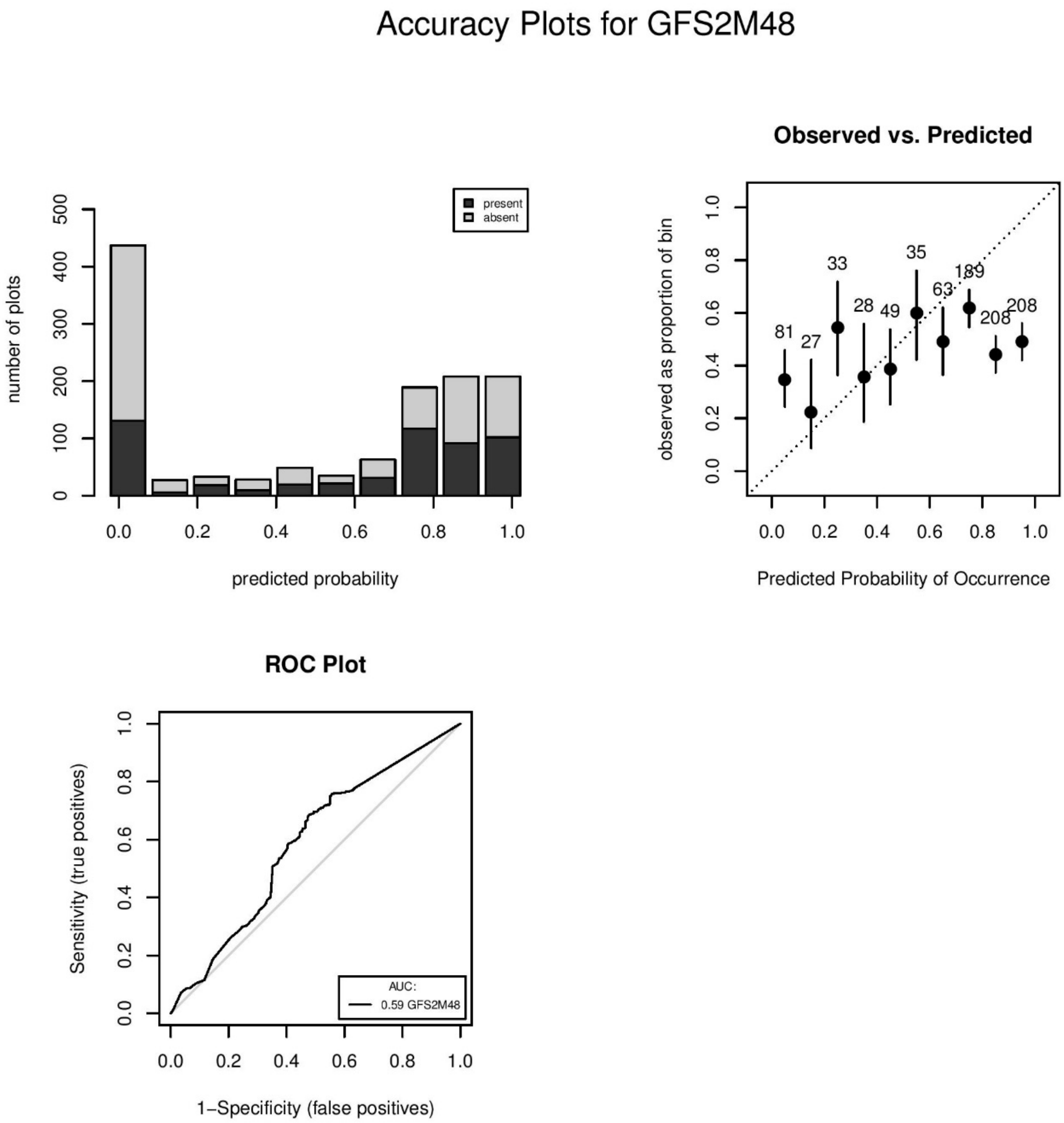
Accuracy Plots for GFS2M46



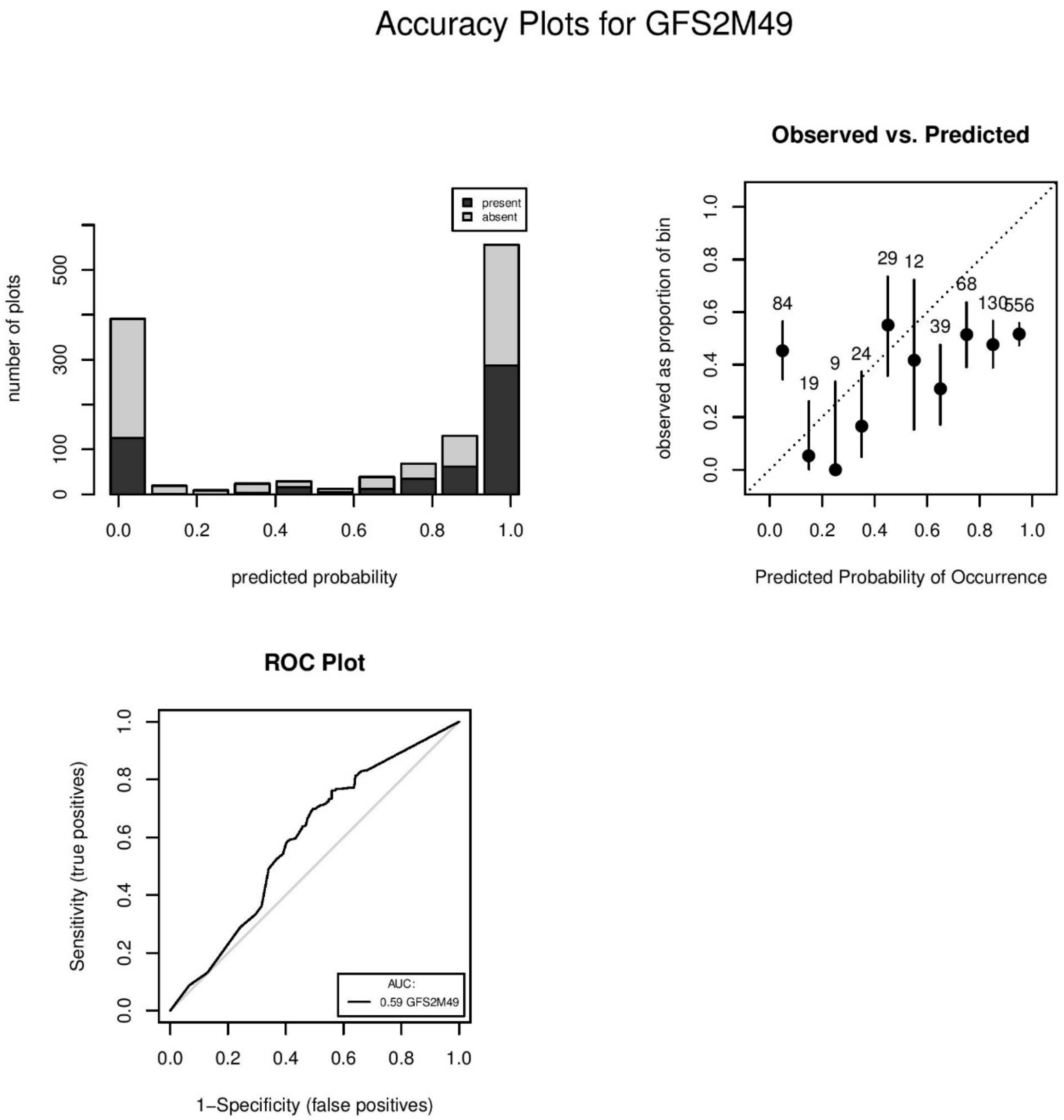


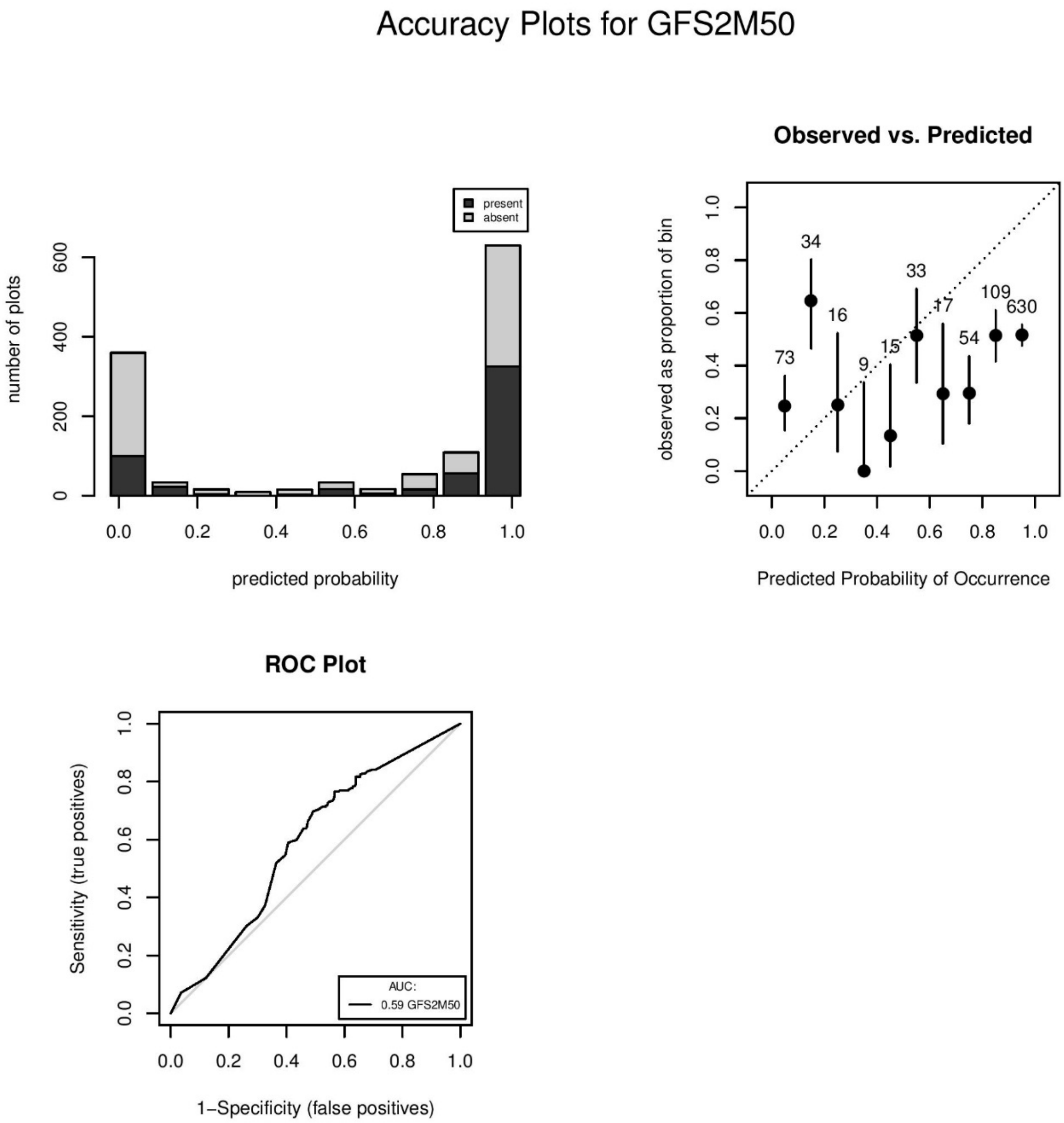



Accuracy Plots for GFS2M47
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
0.0
0.2
0.4
0.6
0.8
1.0
78
22
26
31
46
35
60
171
149
303
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.59 GFS2M47
1−Specificity (false positives)

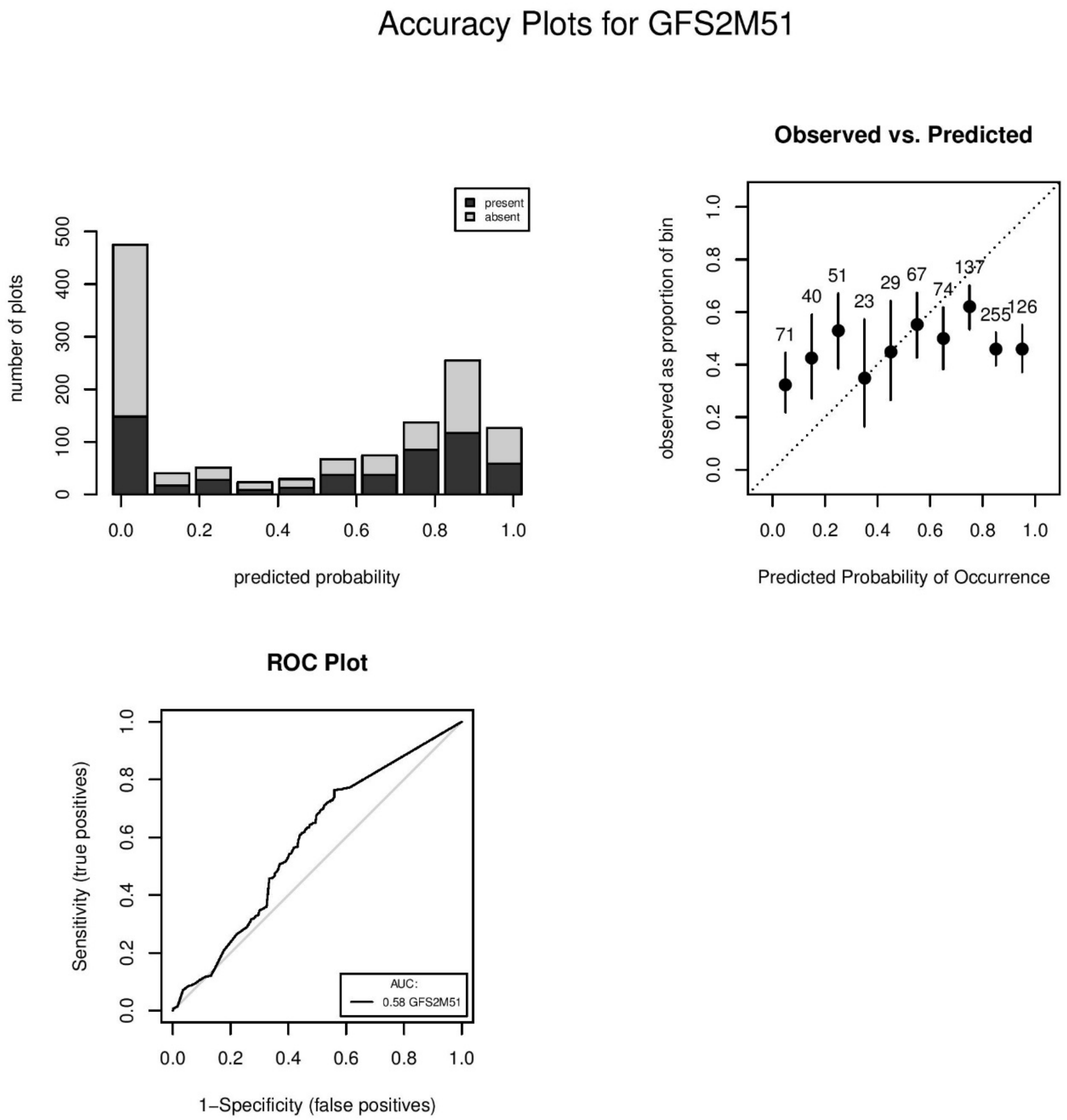


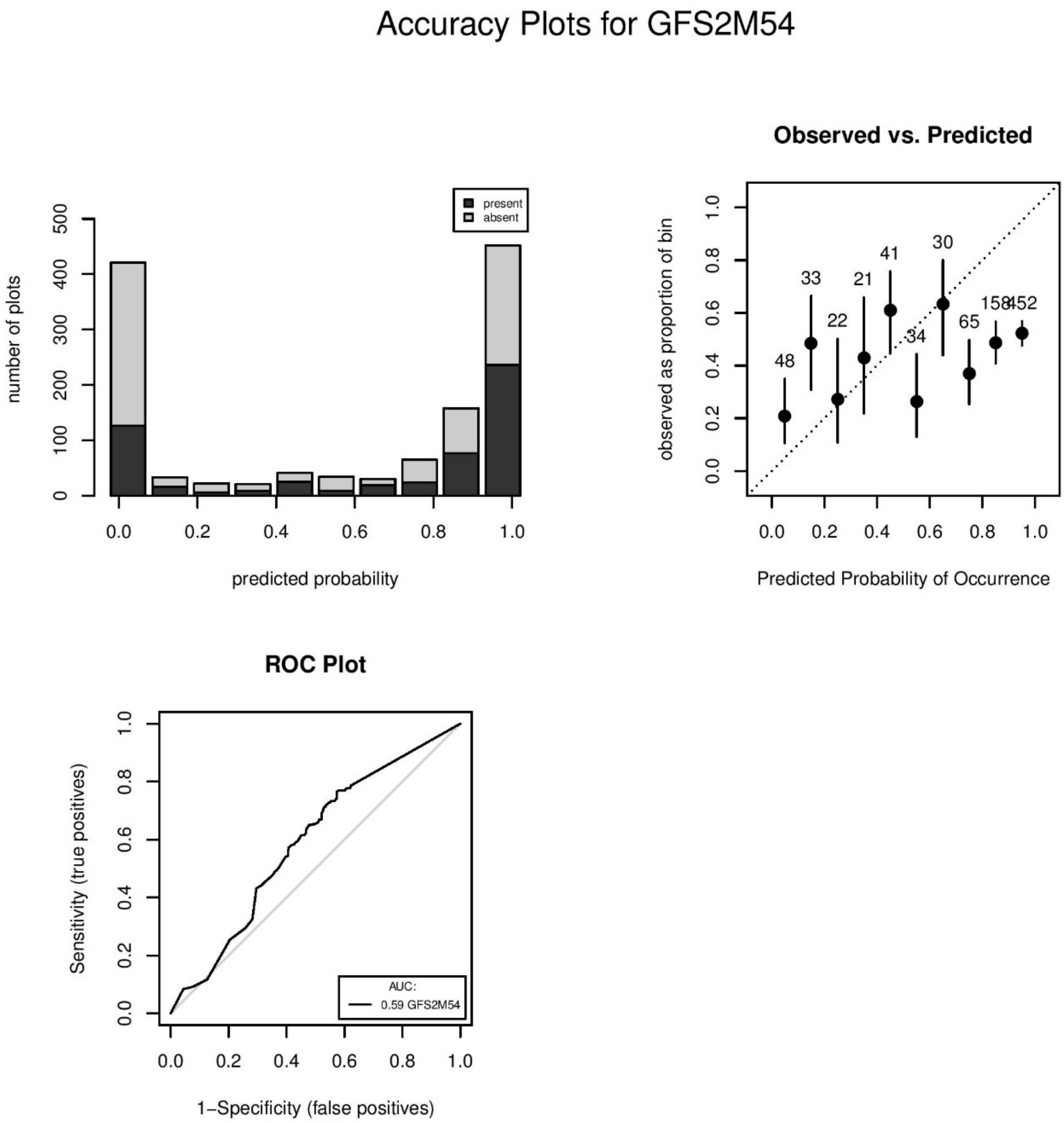
Accuracy Plots for GFS2M48
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
81
27
33
28
49
35
63
189
208
208
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M48


Accuracy Plots for GFS2M49
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
84
19
9
24
29
12
39
68
130
556
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M49

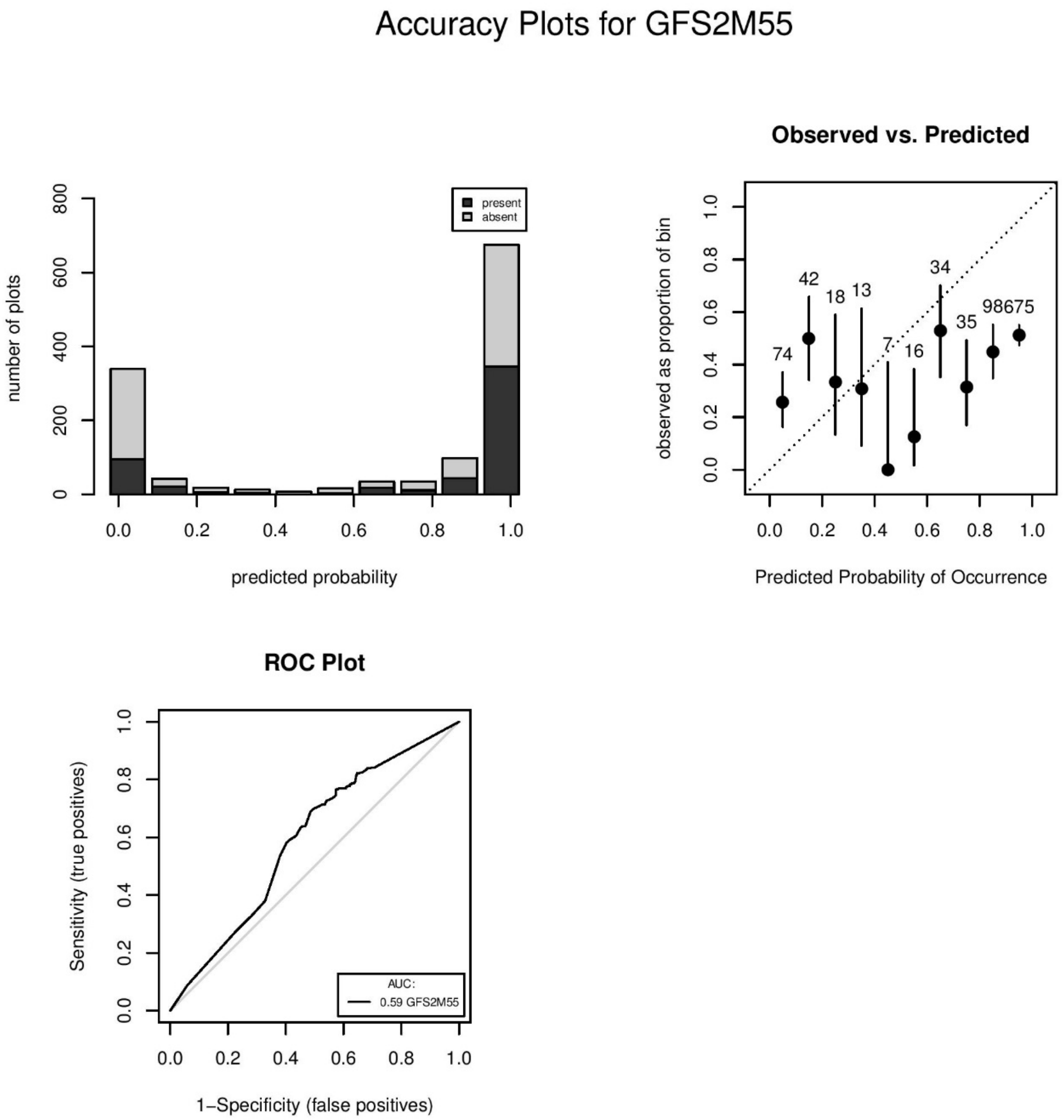


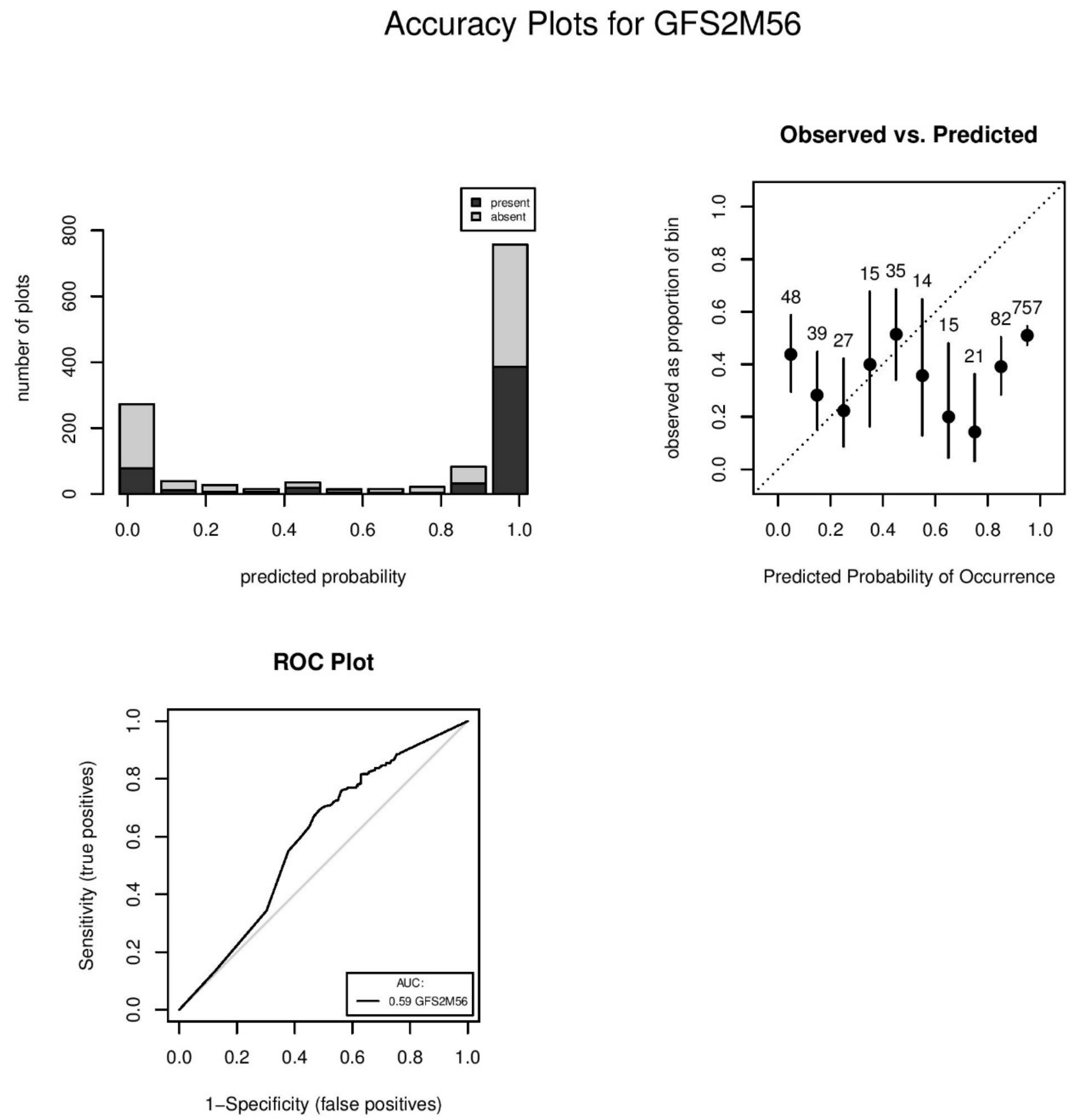
Accuracy Plots for GFS2M50
number of plots
present
absent
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
73
34
16
9
15
33
17
54
109
630
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M50

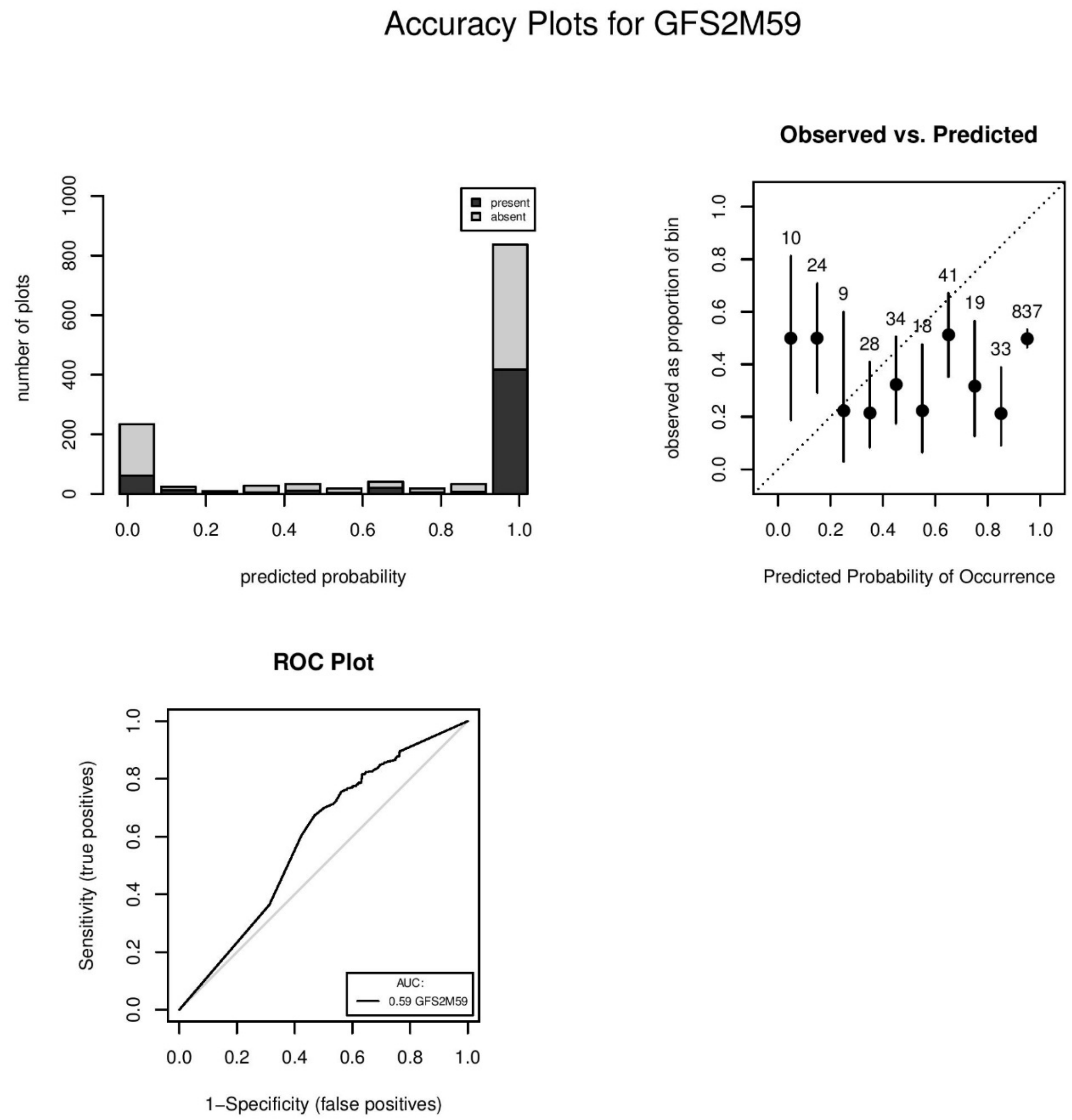

Accuracy Plots for GFS2M51
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
71
40
51
23
29
67
74
137
255
126
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS2M51



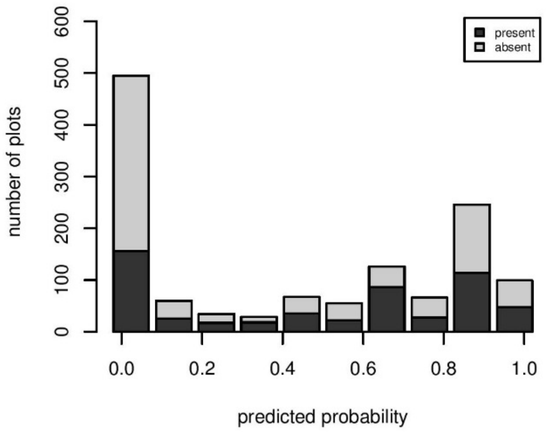
Accuracy Plots for GFS2M54
Observed vs. Predicted
present
absent
number of plots
predicted probability
observed as proportion of bin
Predicted Probability of Occurrence
48
33
22
21
41
34
30
65
158
452
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M54

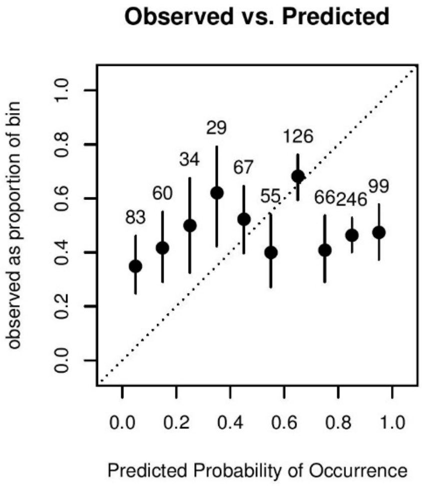

Accuracy Plots for GFS2M55
number of plots
0
200
400
600
800
present
absent
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
0.0
0.2
0.4
0.6
0.8
1.0
74
42
18
13
7
16
34
35
98675
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.59 GFS2M55
1−Specificity (false positives)

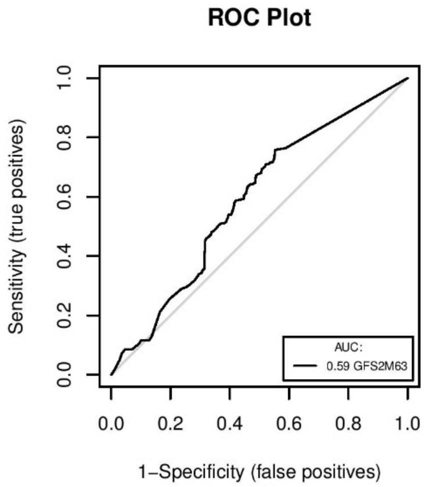

Accuracy Plots for GFS2M56
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
48
39
27
15
35
14
15
21
82
757
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M56

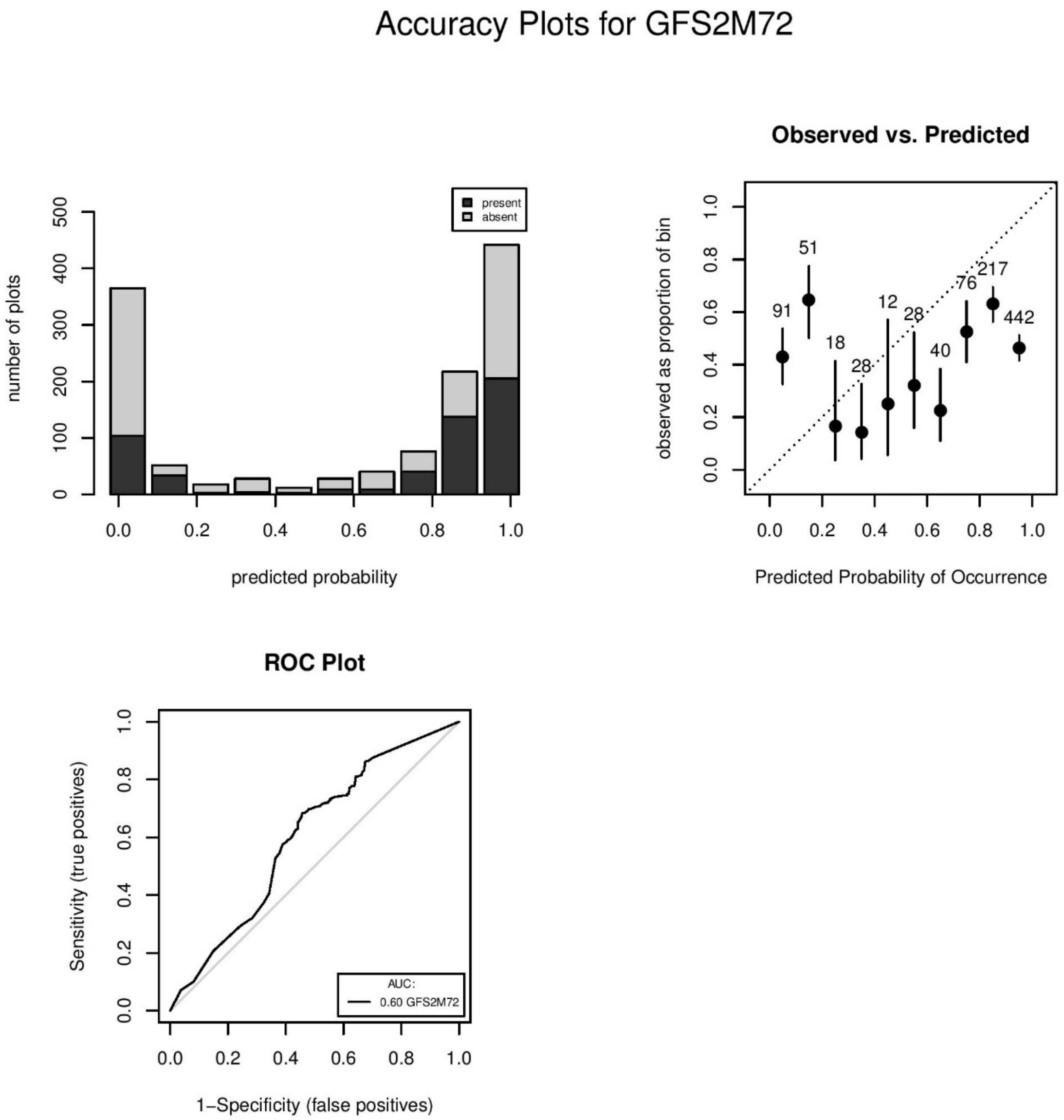

Accuracy Plots for GFS2M59
present
absent
number of plots
0
200
400
600
800
1000
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
10
24
9
28
34
18
41
19
33
837
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M59

Accuracy Plots for GFS2M63

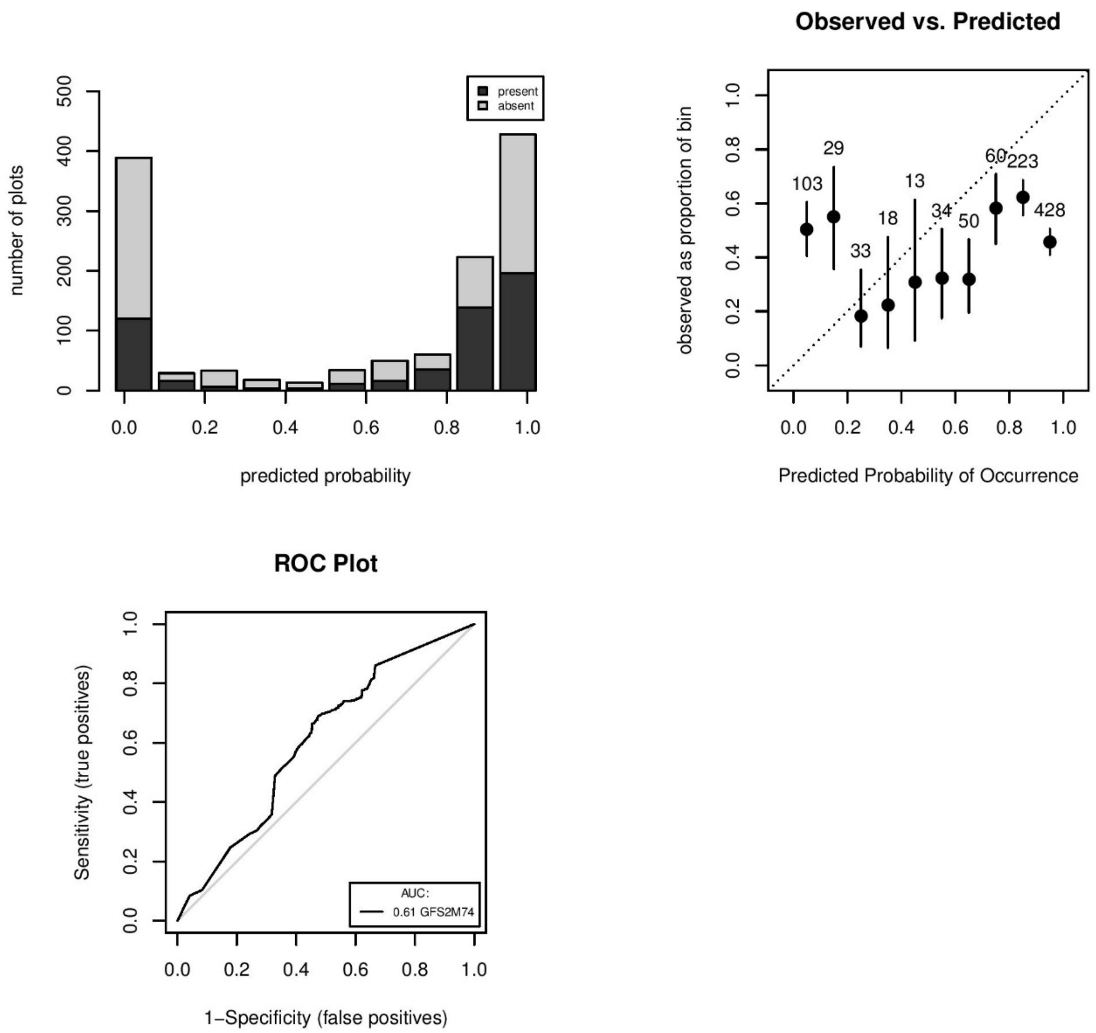


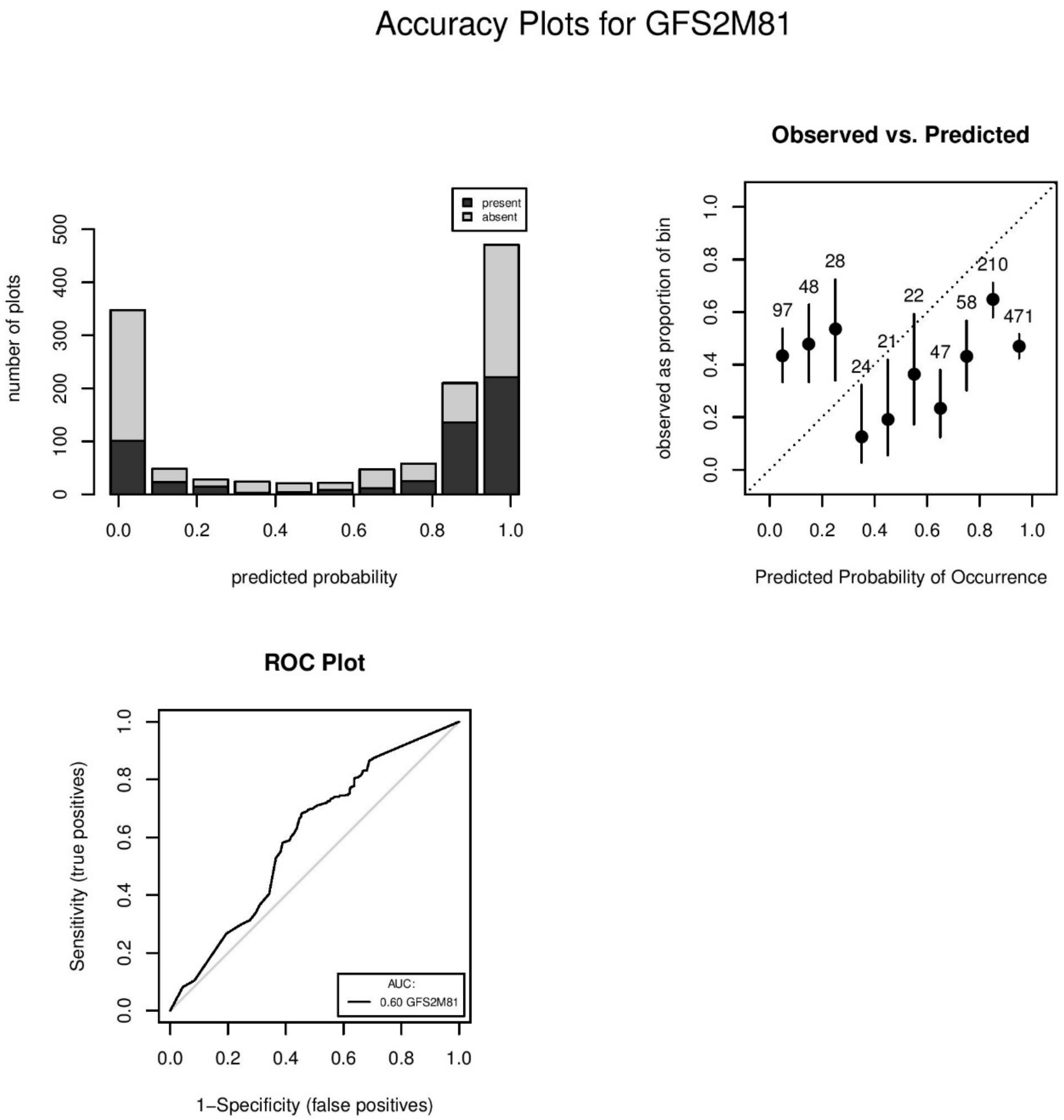


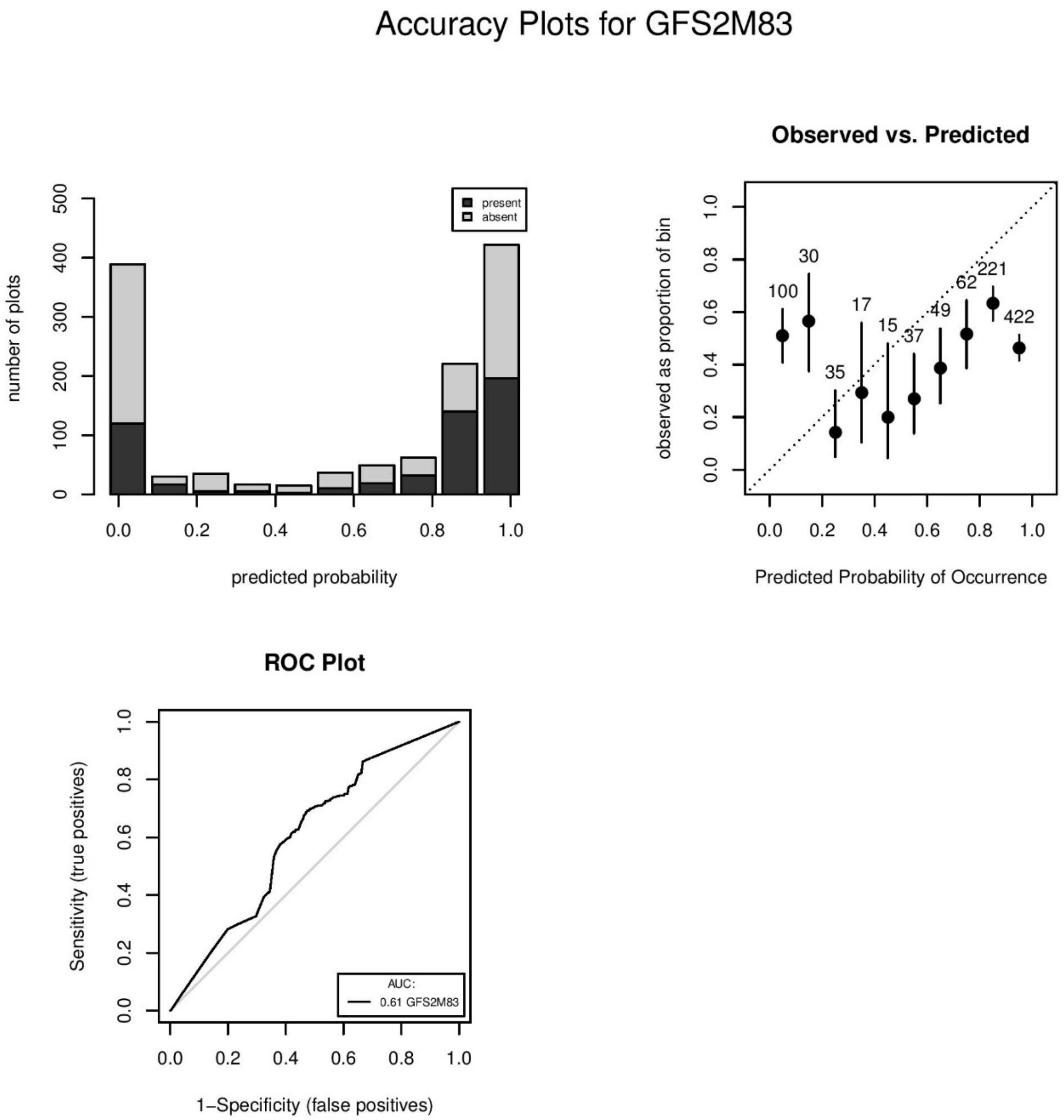


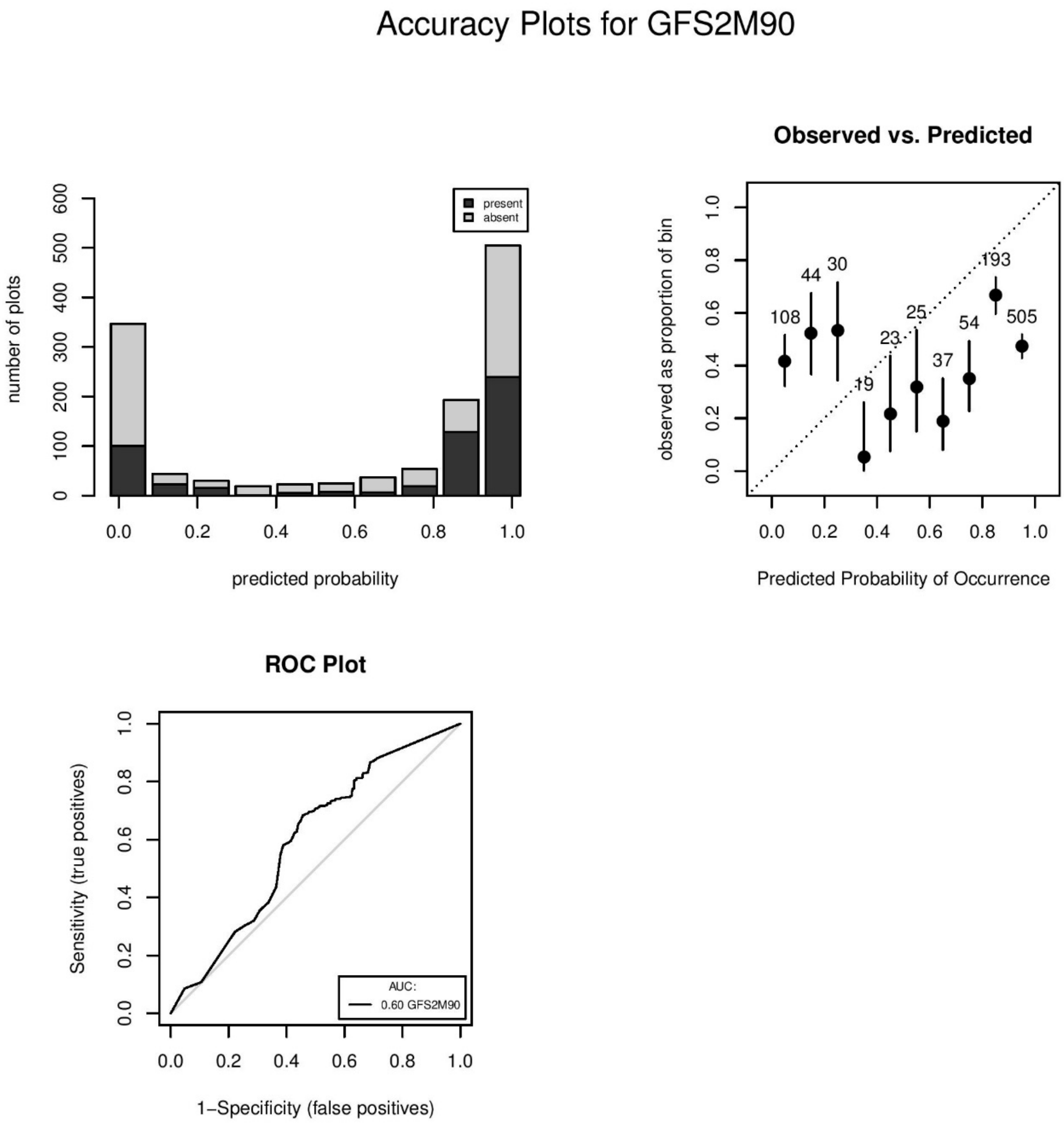

Accuracy Plots for GFS2M72
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
91
51
18
28
12
28
40
76
217
442
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M72

Accuracy Plots for GFS2M74

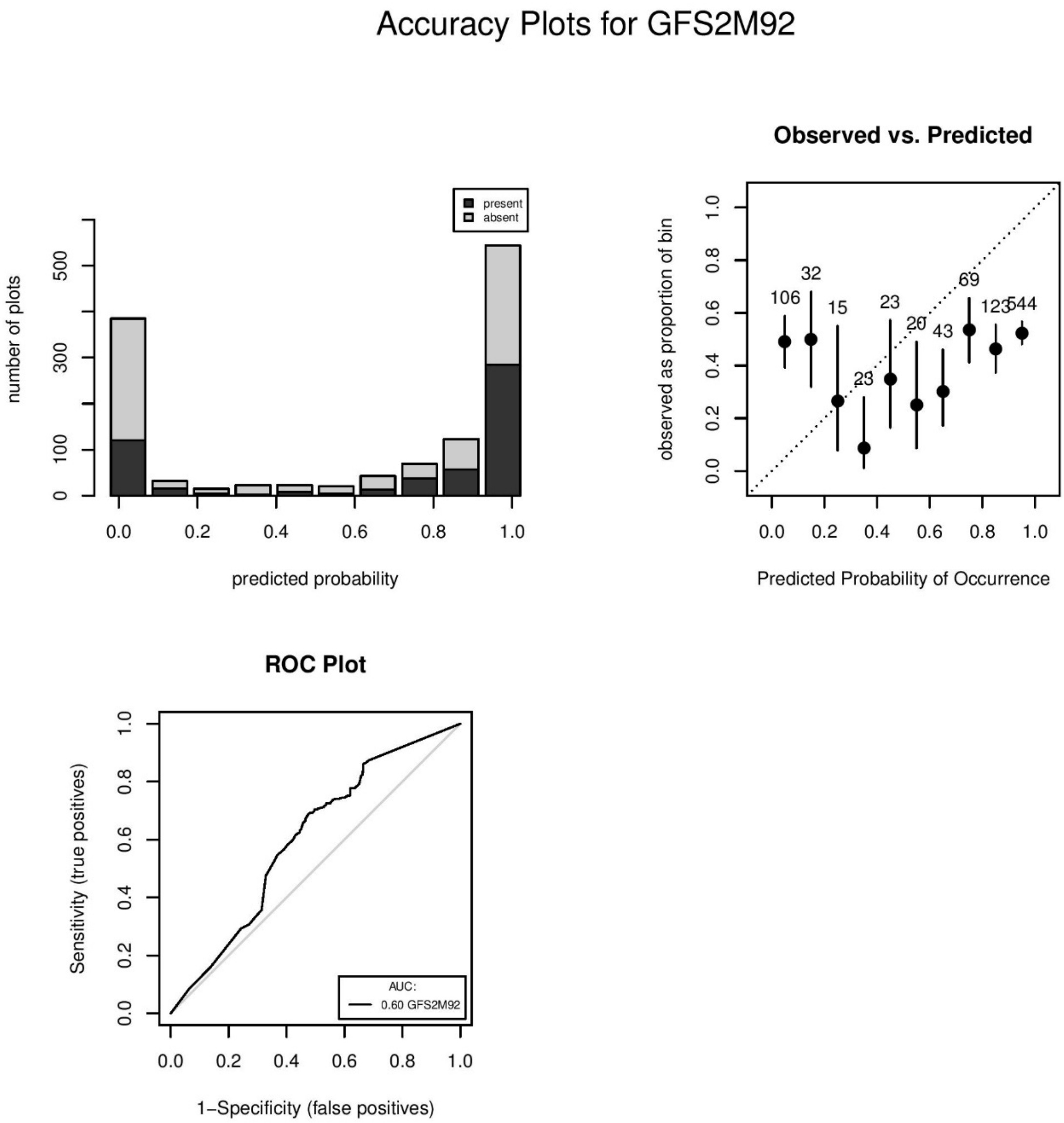



Accuracy Plots for GFS2M81
Observed vs. Predicted
present
absent
number of plots
predicted probability
observed as proportion of bin
Predicted Probability of Occurrence
97
48
28
24
21
22
47
58
210
471
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M81

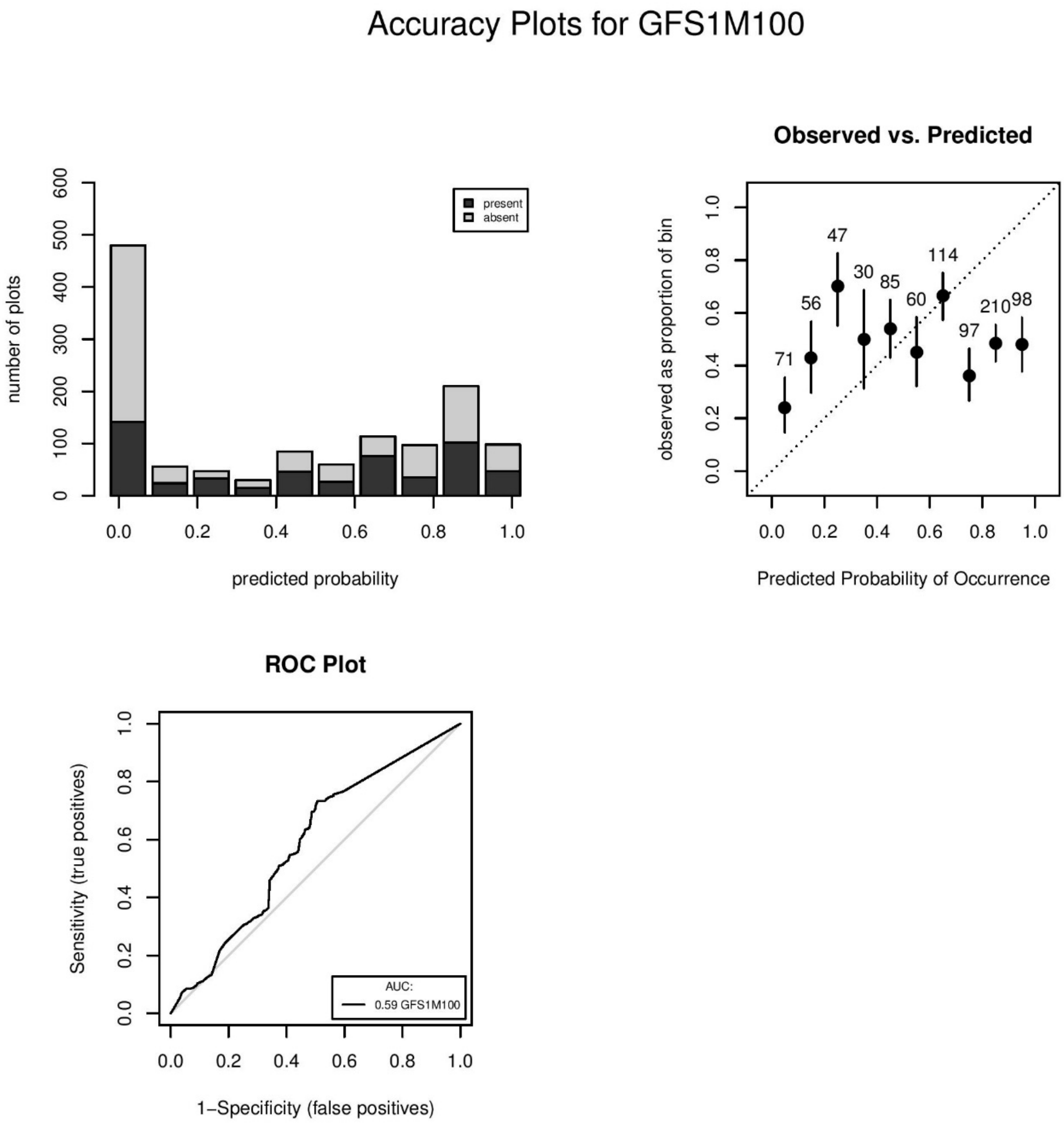

Accuracy Plots for GFS2M83
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
100
30
35
17
15
37
49
62
221
422
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.61 GFS2M83

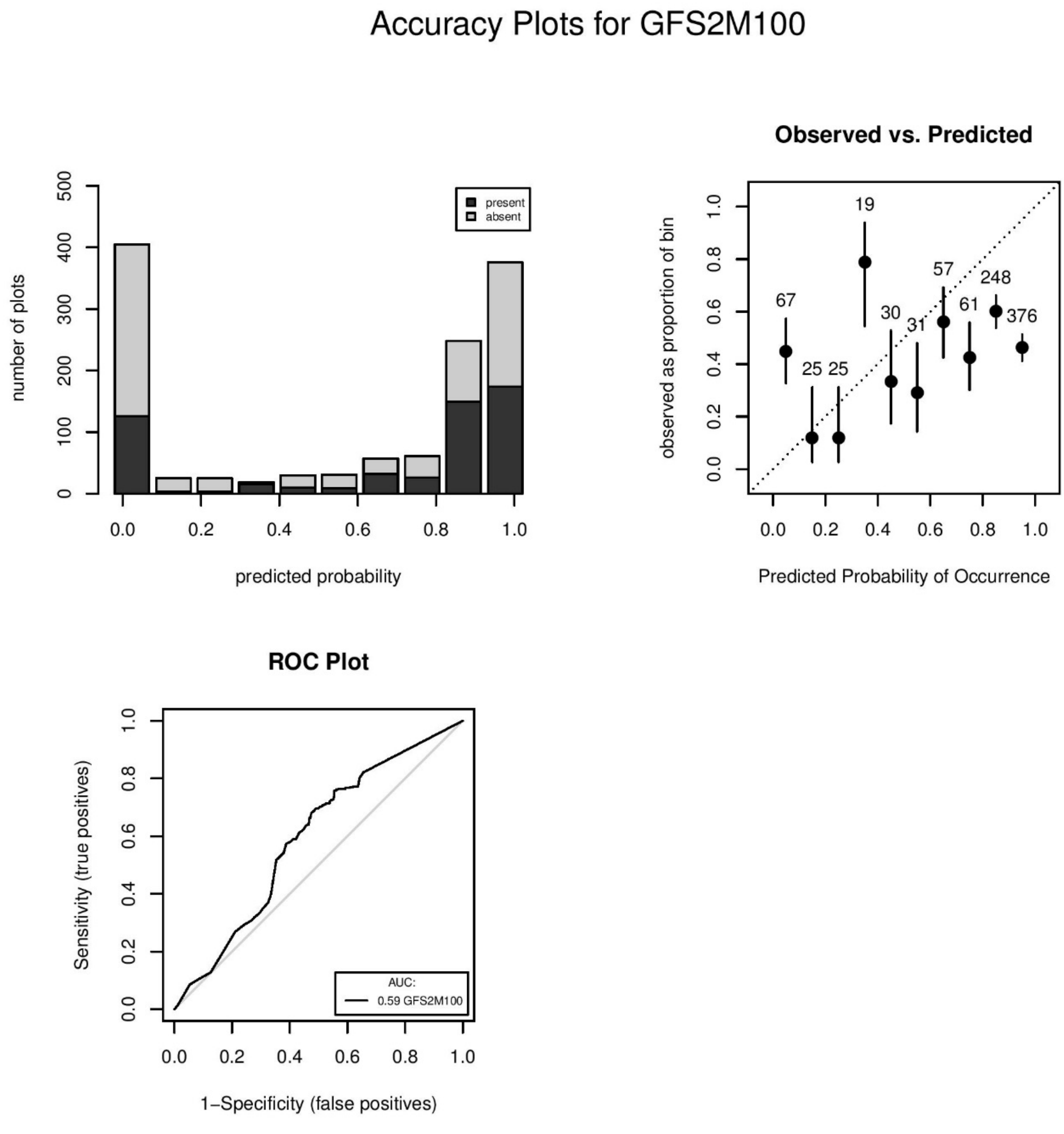


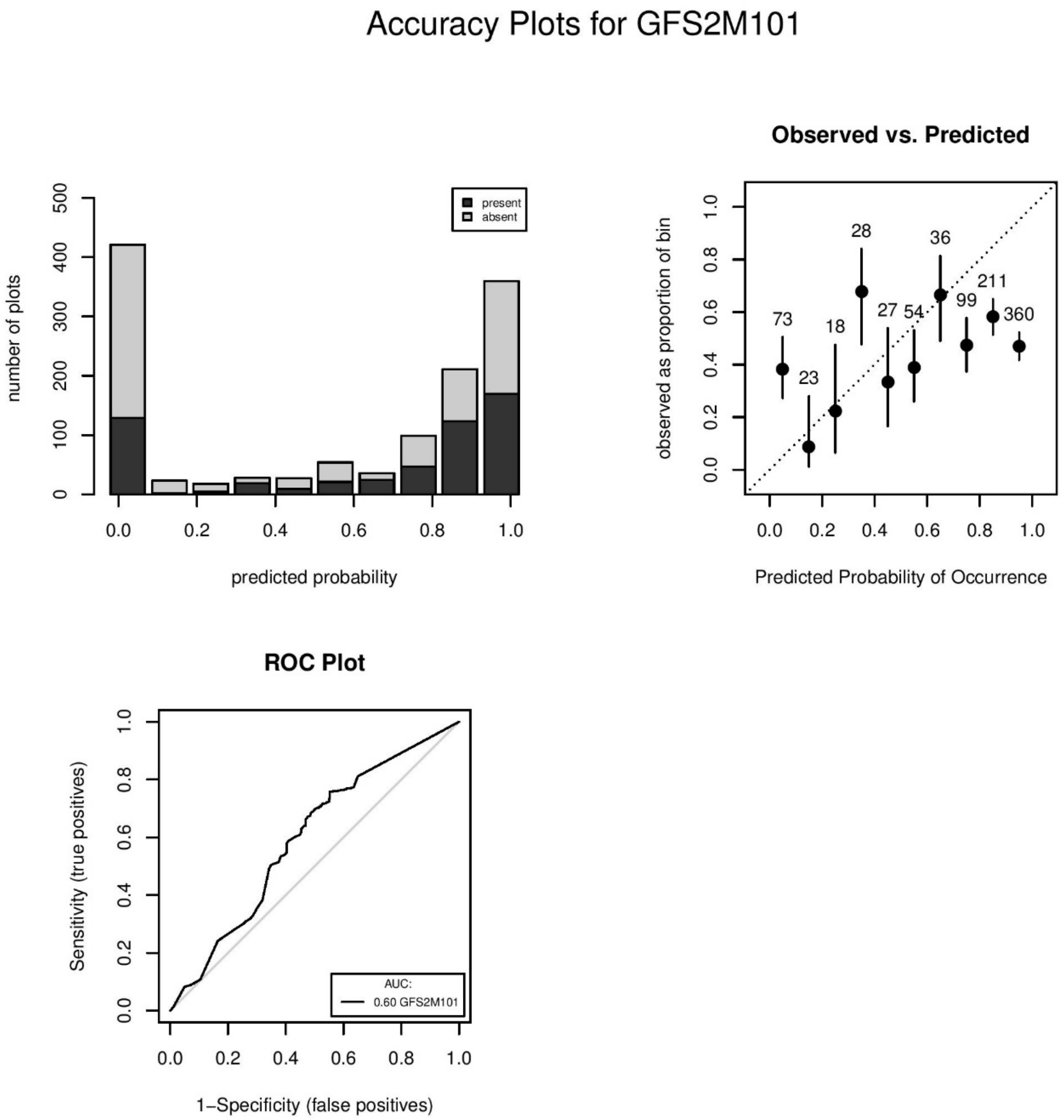
Accuracy Plots for GFS2M90
number of plots
0
100
200
300
400
500
600
present
absent
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
0.0
0.2
0.4
0.6
0.8
1.0
108
44
30
19
23
25
37
54
193
505
0.0
0.2
0.4
0.6
0.8
1.0
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
0.0
0.2
0.4
0.6
0.8
1.0
AUC:
0.60 GFS2M90
0.0
0.2
0.4
0.6
0.8
1.0
1−Specificity (false positives)



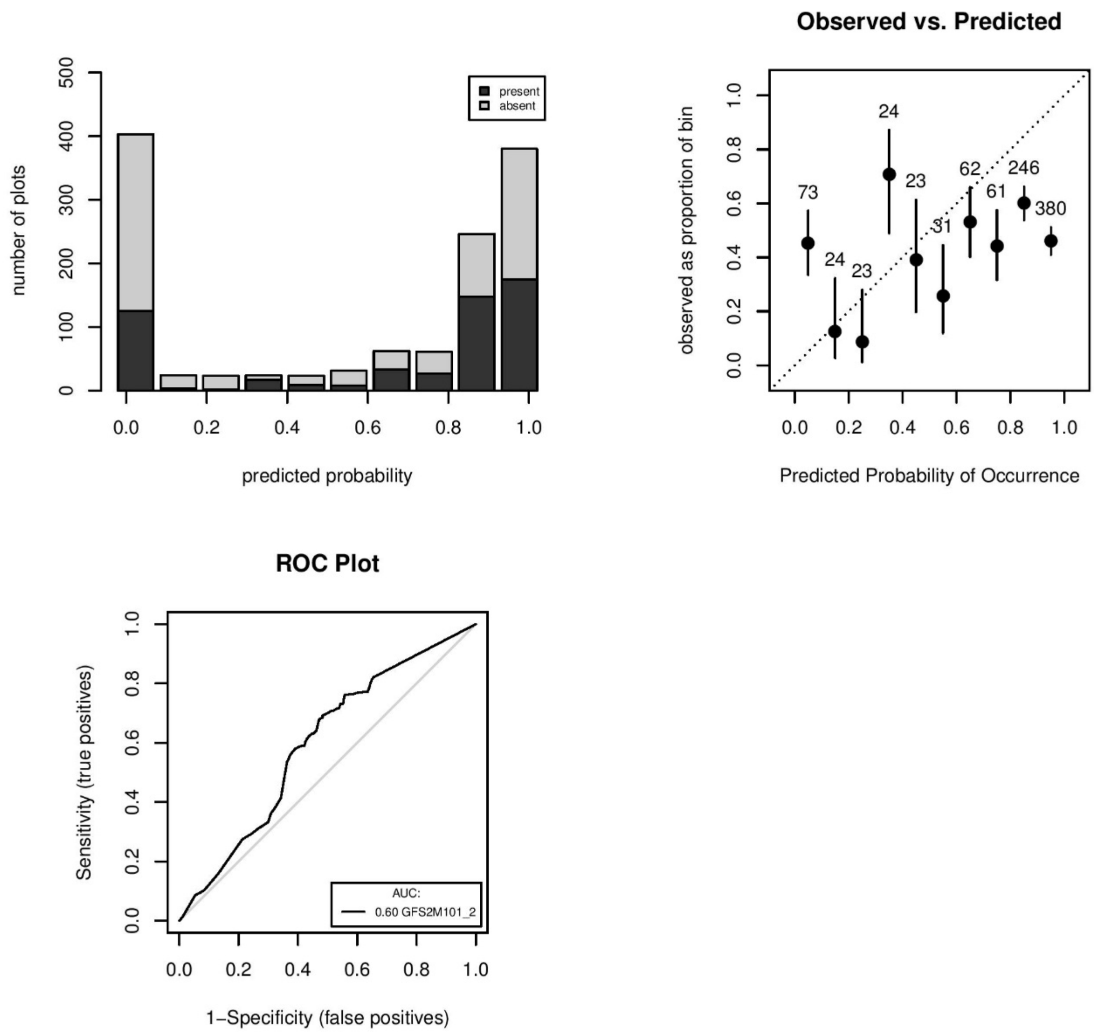
Accuracy Plots for GFS2M92
present
absent
number of plots
0
100
300
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
106
32
15
23
23
20
43
69
123
544
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M92

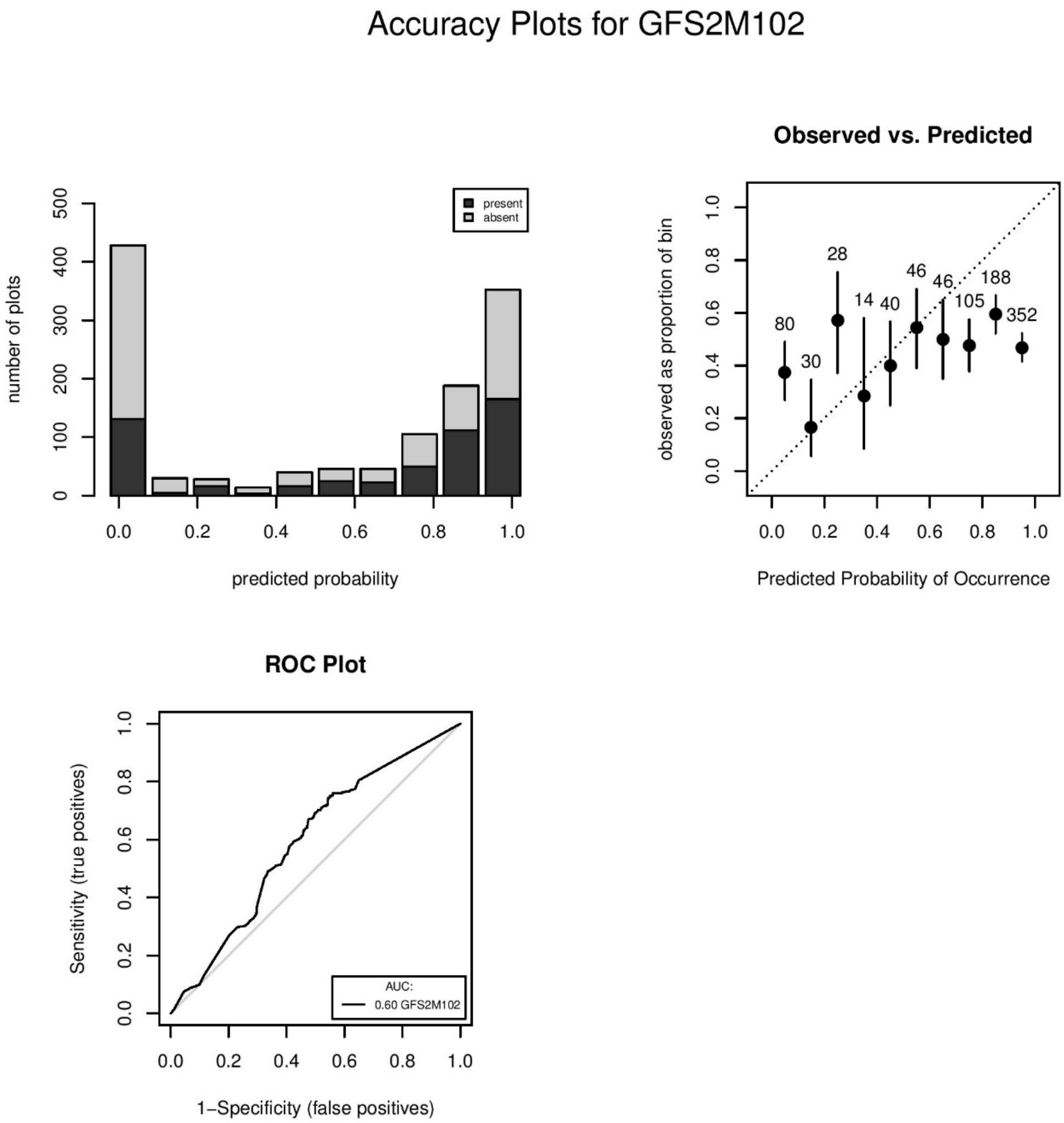

Accuracy Plots for GFS1M100
number of plots
predicted probability
present
absent
0
100
200
300
400
500
600
0.0
0.2
0.4
0.6
0.8
1.0
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
71
56
47
30
85
60
114
97
210
98
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS1M100


Accuracy Plots for GFS2M100
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
67
25 25
19
30
31
57
61
248
376
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M100

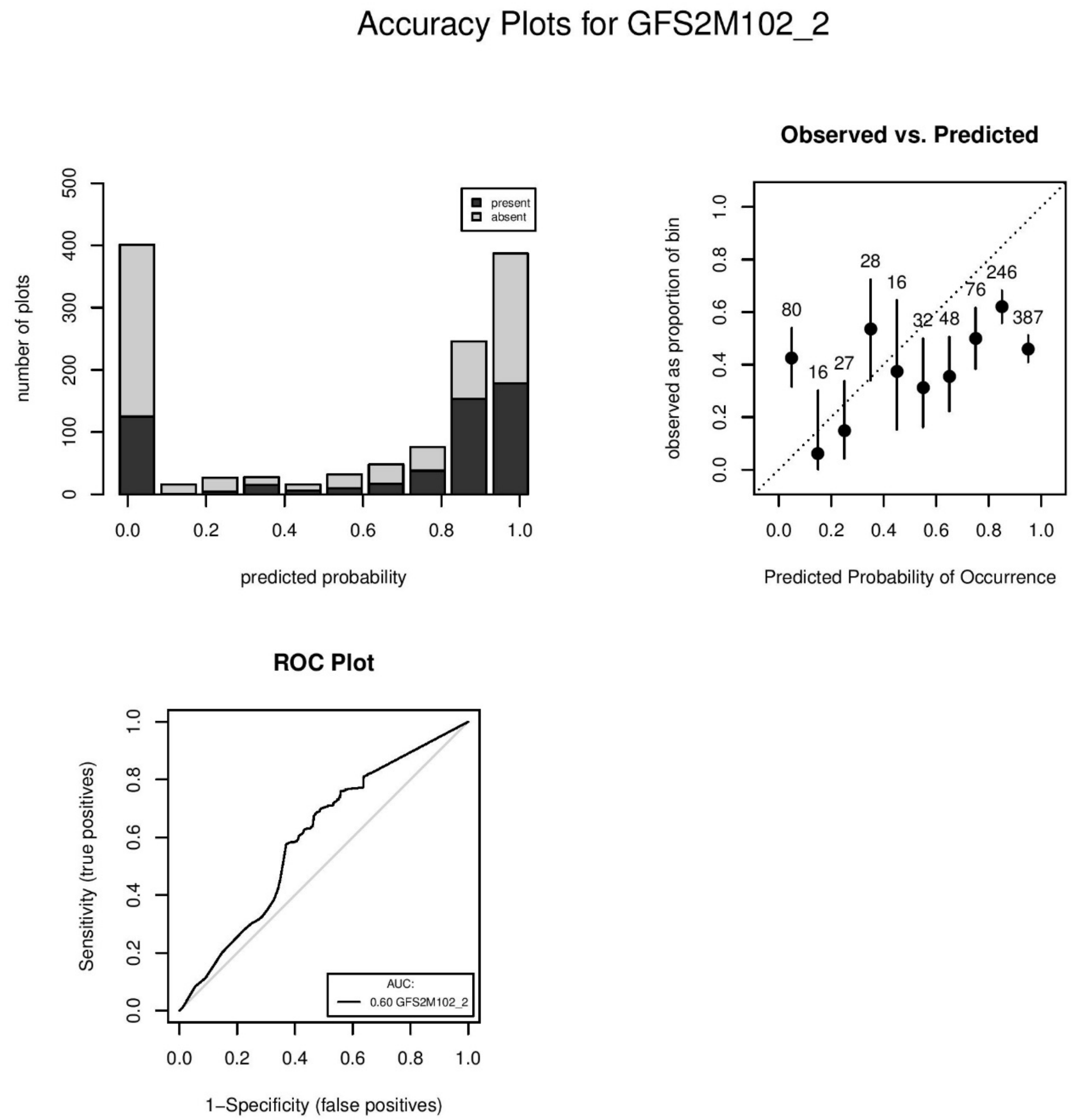

Accuracy Plots for GFS2M101
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
73
23
18
28
27
54
36
99
211
360
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.60 GFS2M101
1−Specificity (false positives)

Accuracy Plots for GFS2M101_2

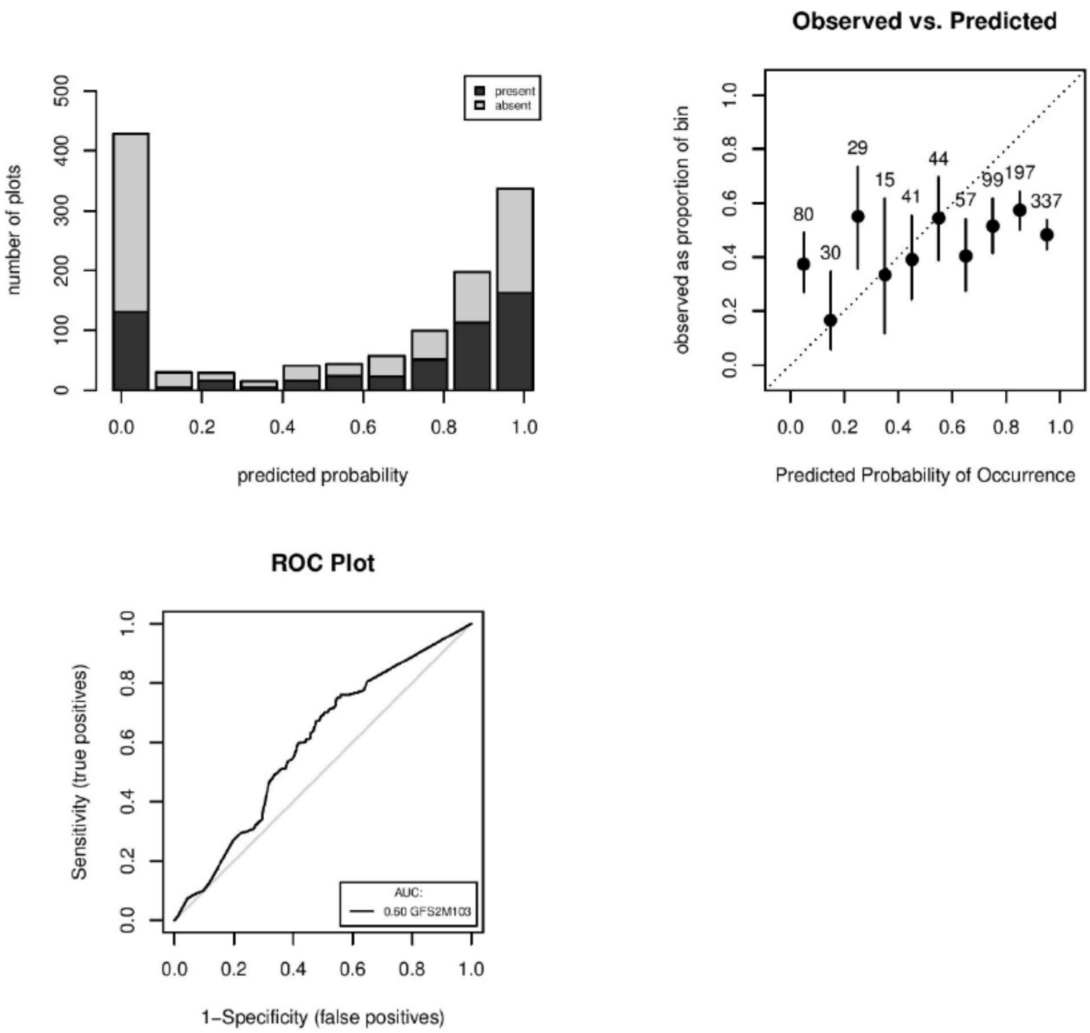


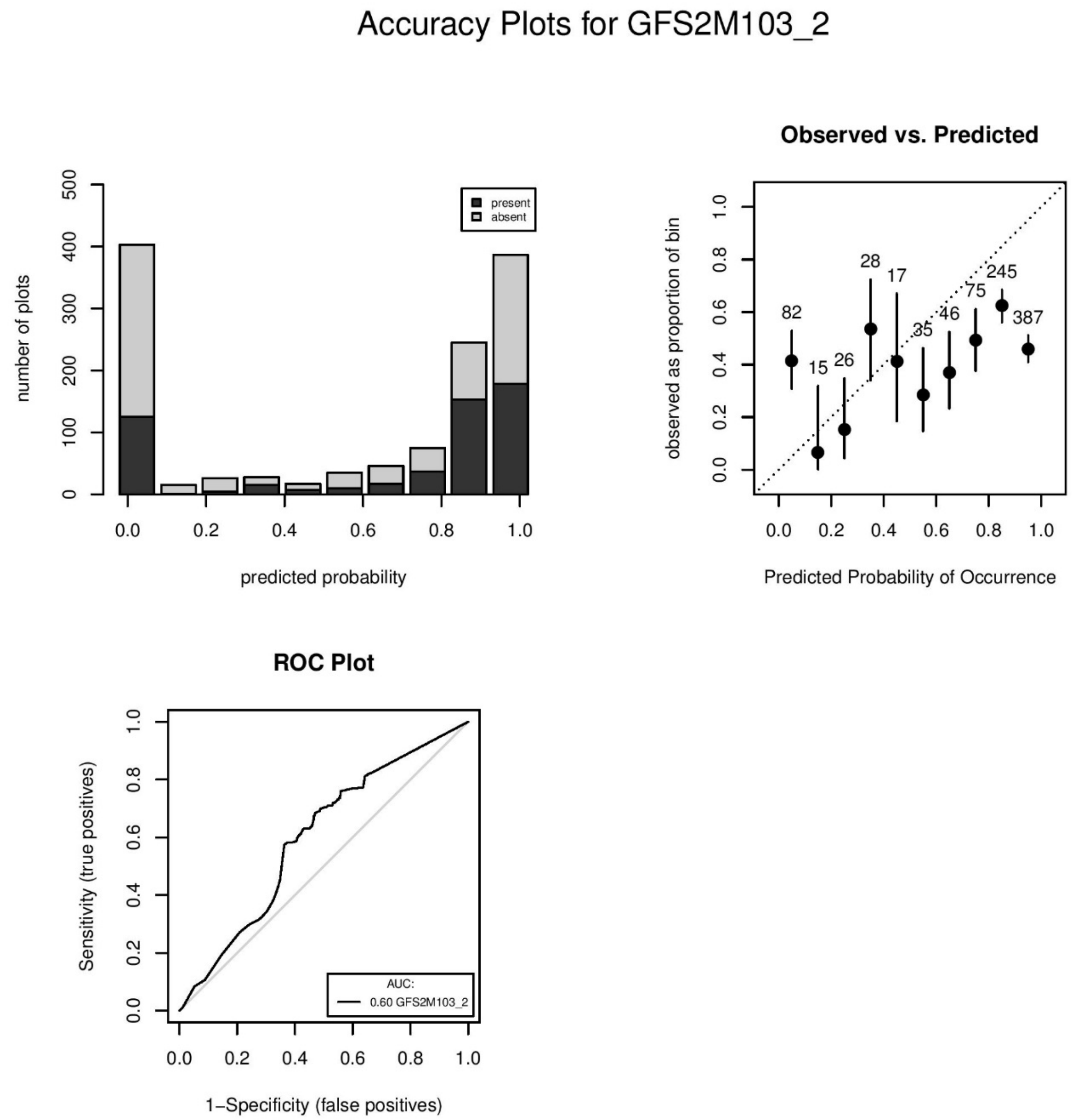


Accuracy Plots for GFS2M102
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
80
30
28
14
40
46
46
105
188
352
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M102

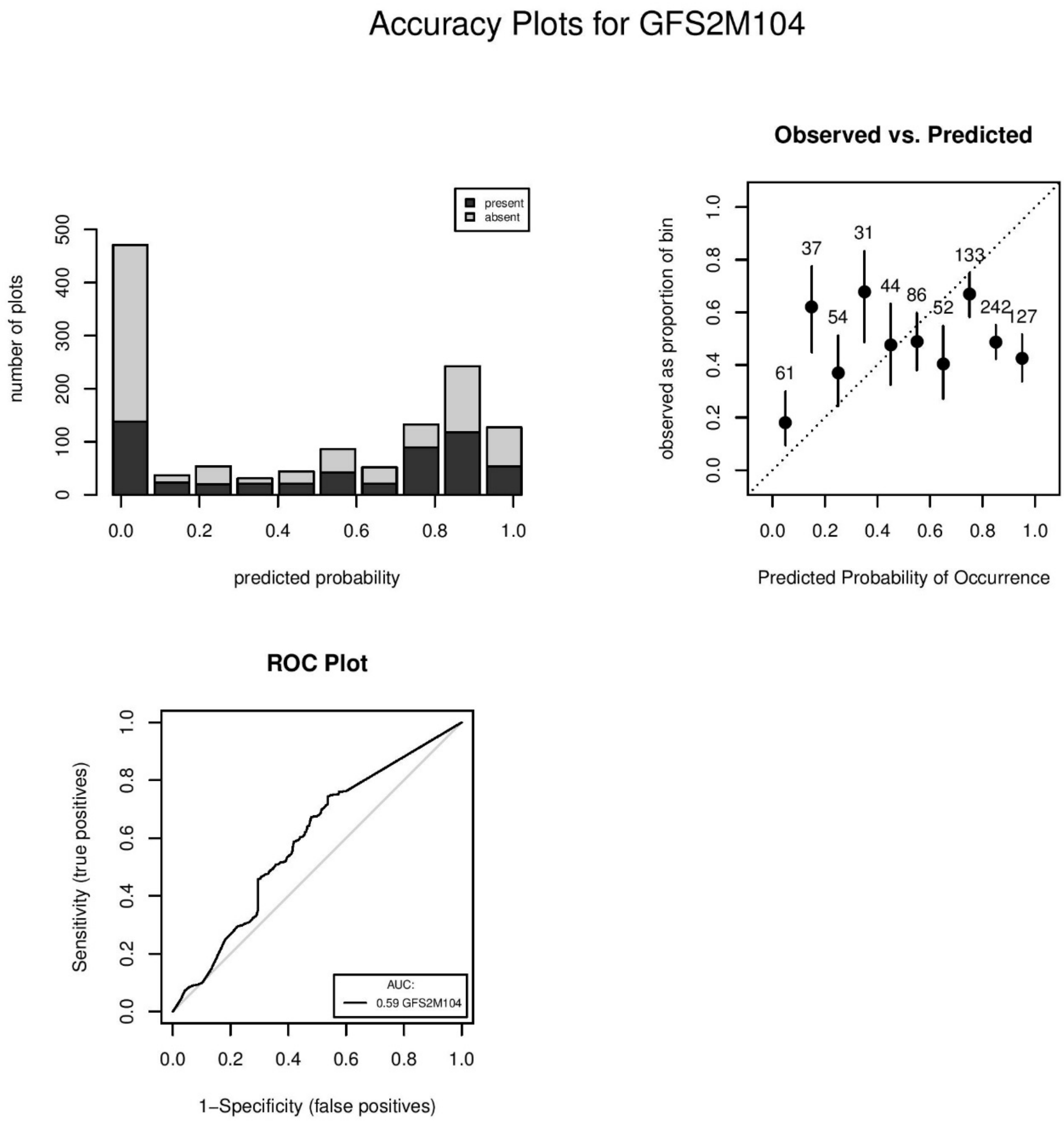

Accuracy Plots for GFS2M102_2
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
80
16
27
28
16
32
48
76
246
387
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M102_2

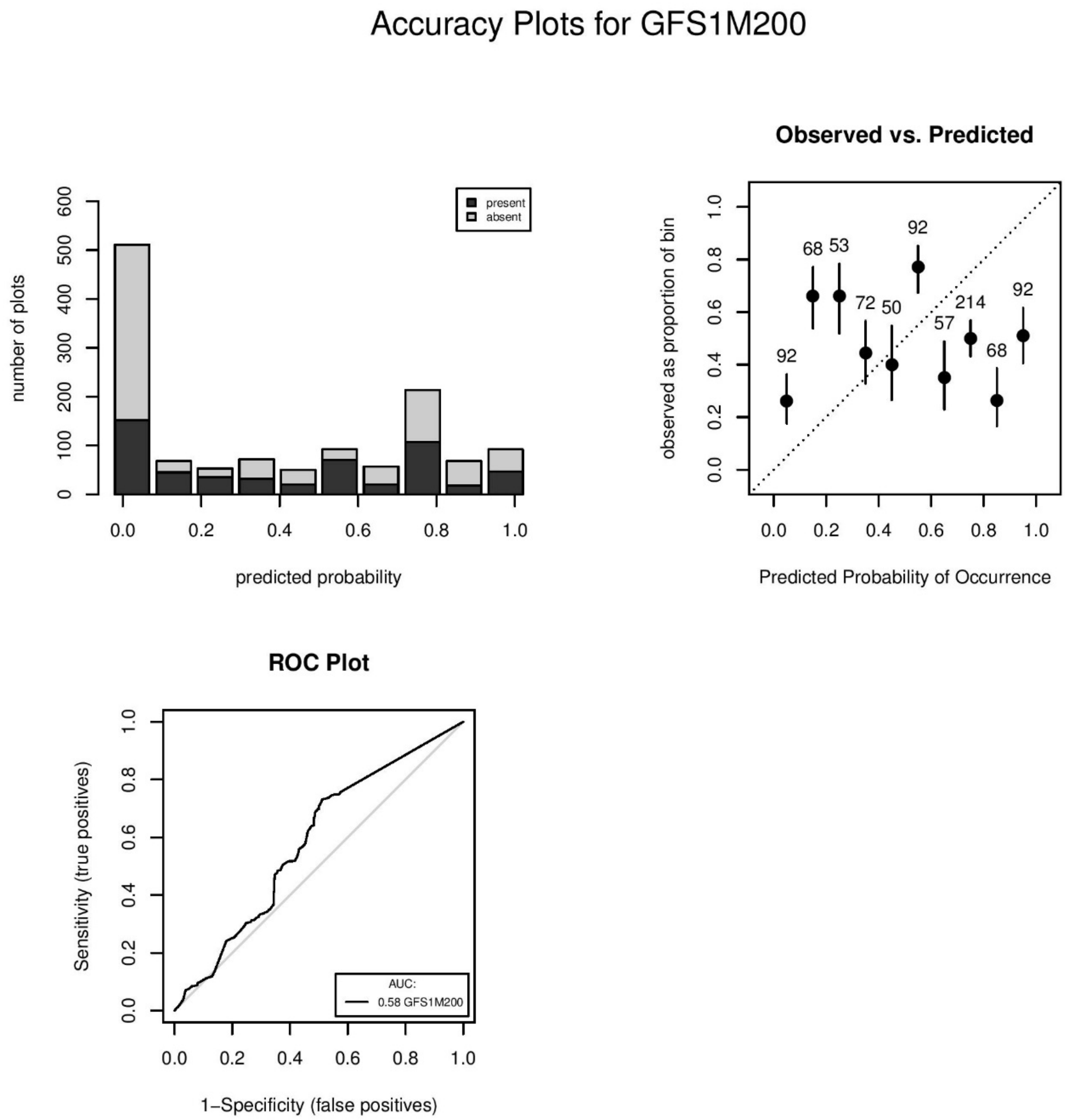
Accuracy Plots for GFS2M103

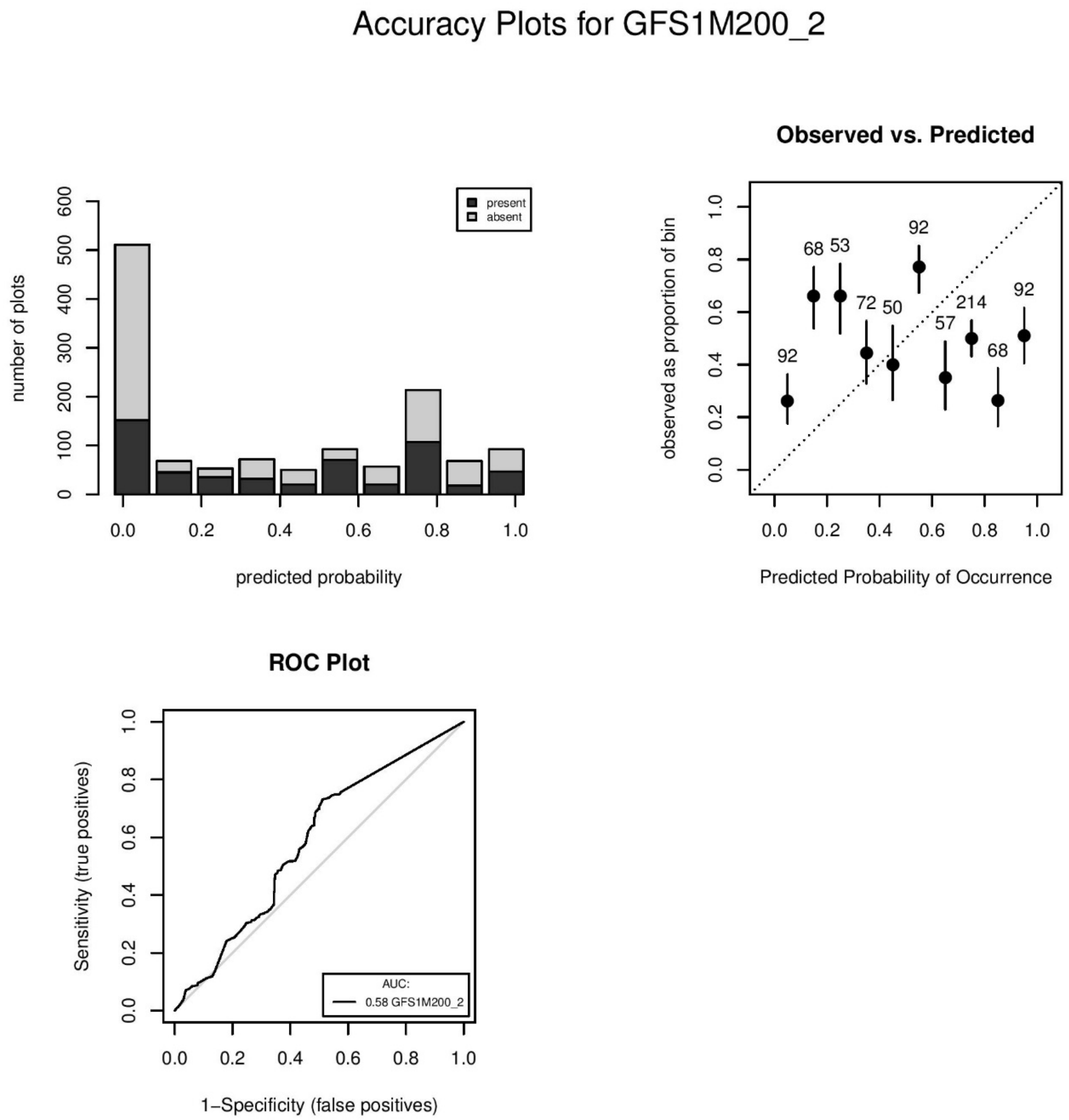




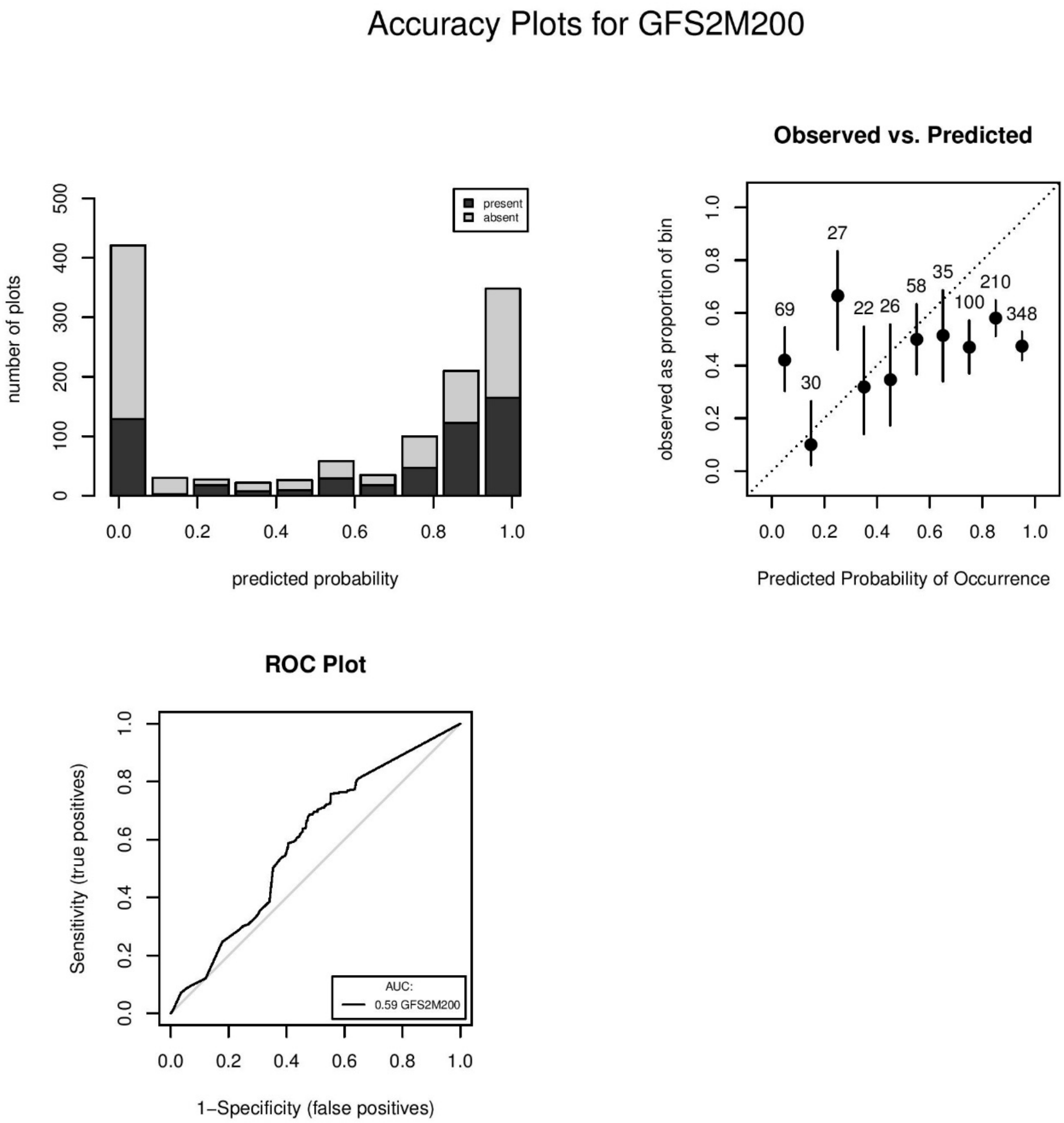
Accuracy Plots for GFS2M103_2
number of plots
predicted probability
present
absent
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
82
15
26
28
17
35
46
75
245
387
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.60 GFS2M103_2

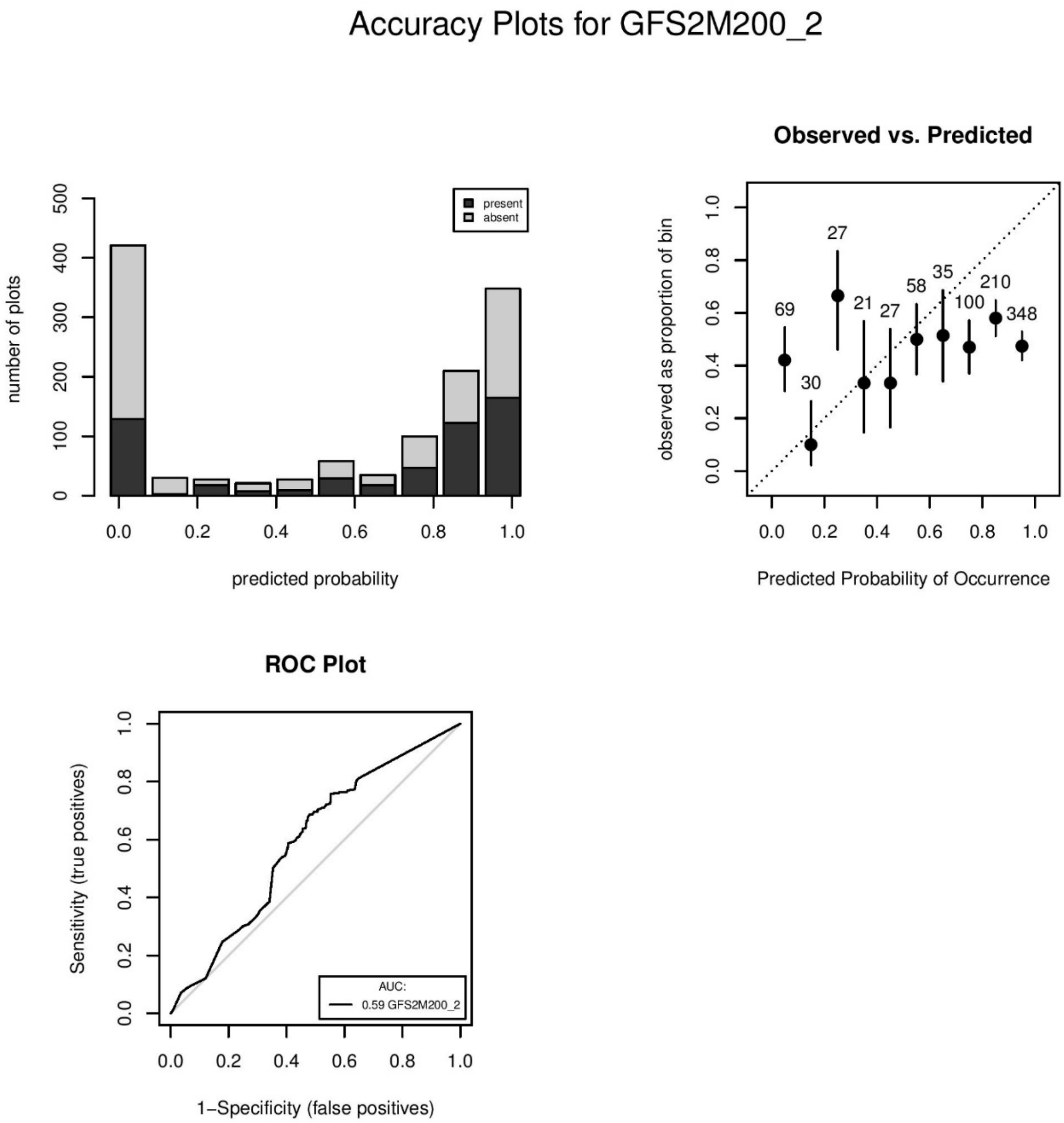

Accuracy Plots for GFS2M104
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
61
37
54
31
44
86
52
133
242
127
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M104

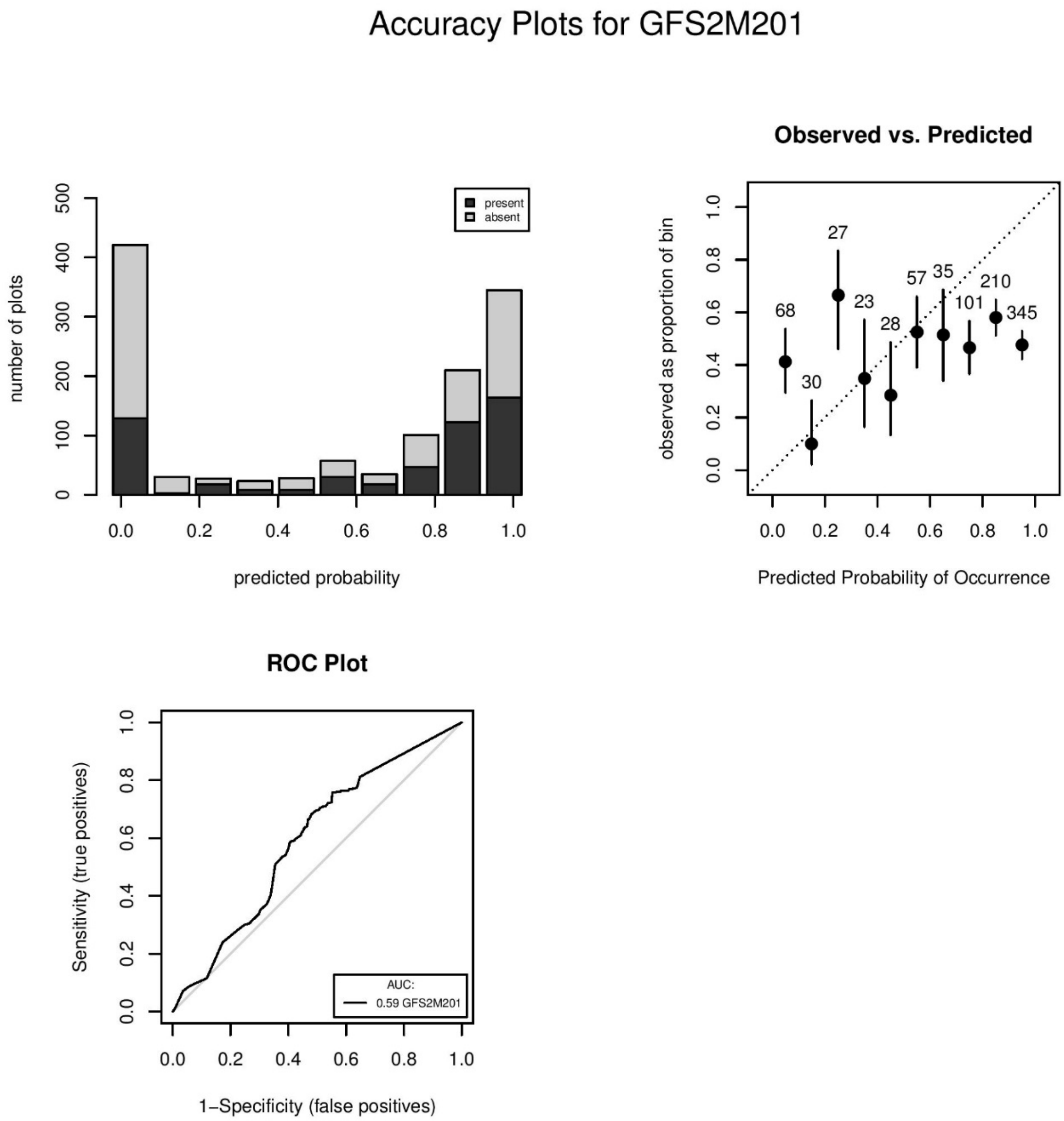

Accuracy Plots for GFS1M200
number of plots
predicted probability
present
absent
0
100
200
300
400
500
600
0.0
0.2
0.4
0.6
0.8
1.0
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
92
68
53
72
50
92
57
214
68
92
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M200



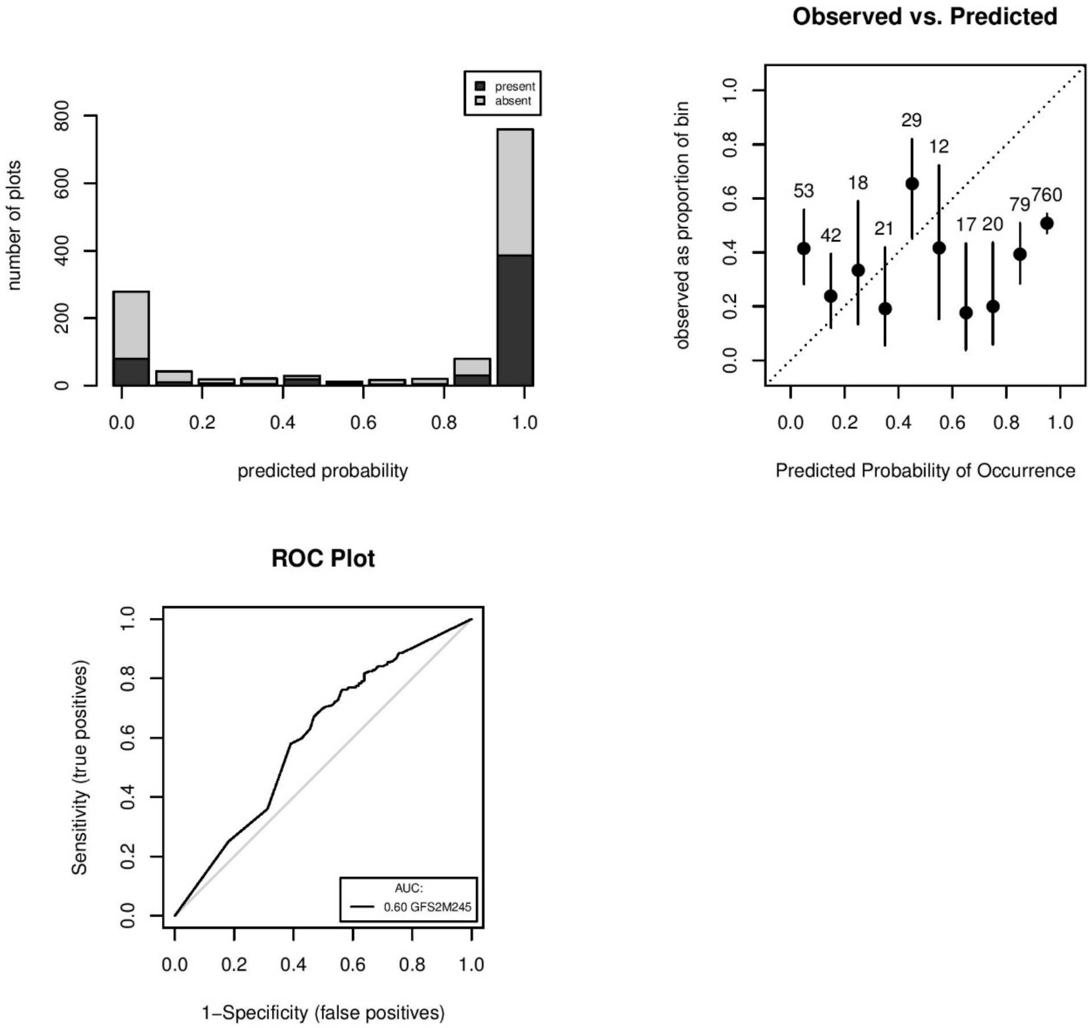
Accuracy Plots for GFS1M200_2
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
92
68
53
72
50
92
57
214
68
92
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 GFS1M200_2

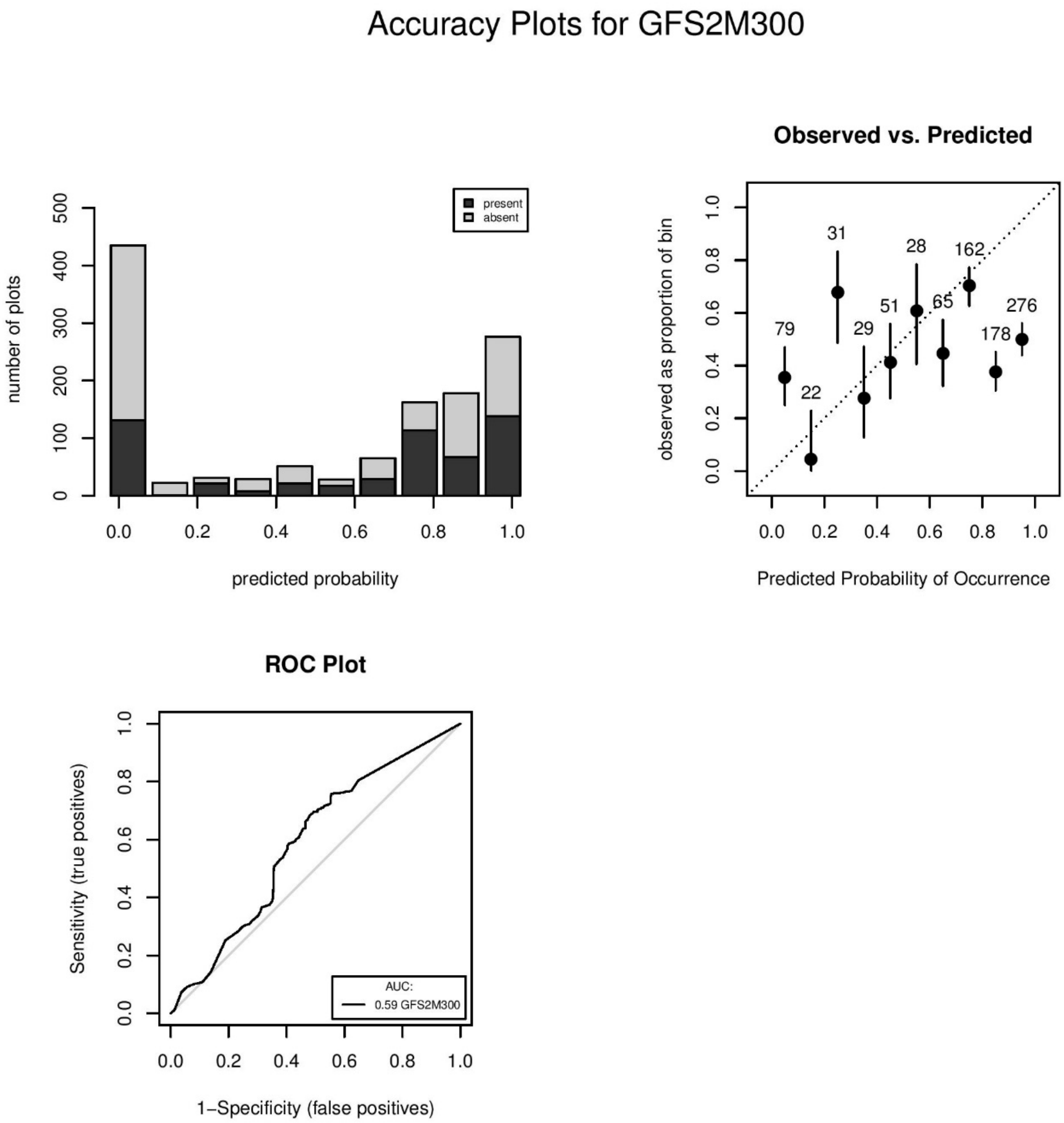

Accuracy Plots for GFS2M200
number of plots
present
absent
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
69
30
27
22 26
58
35
100
210
348
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M200


Accuracy Plots for GFS2M200_2
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
69
30
27
21
27
58
35
100
210
348
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M200_2

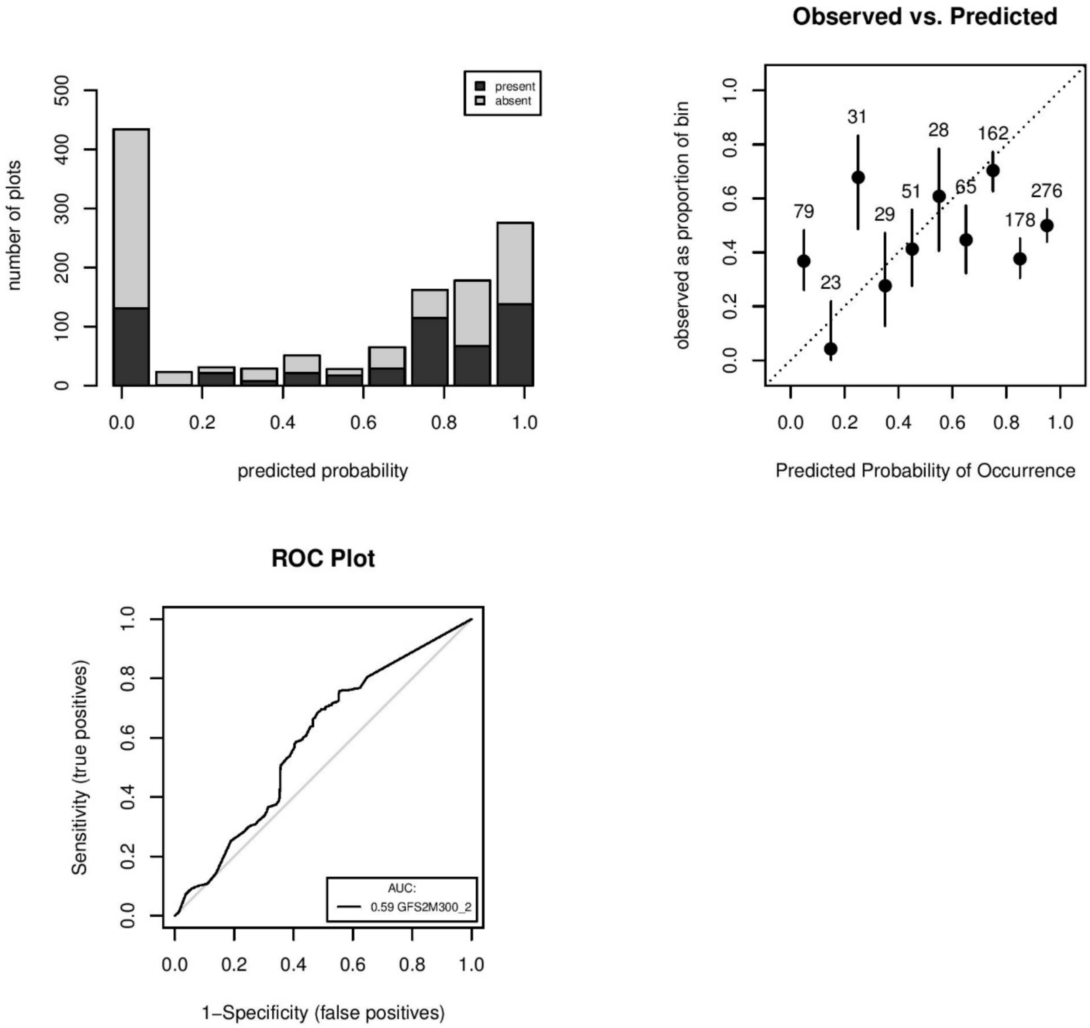

Accuracy Plots for GFS2M201
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
68
30
27
23
28
57
35
101
210
345
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M201

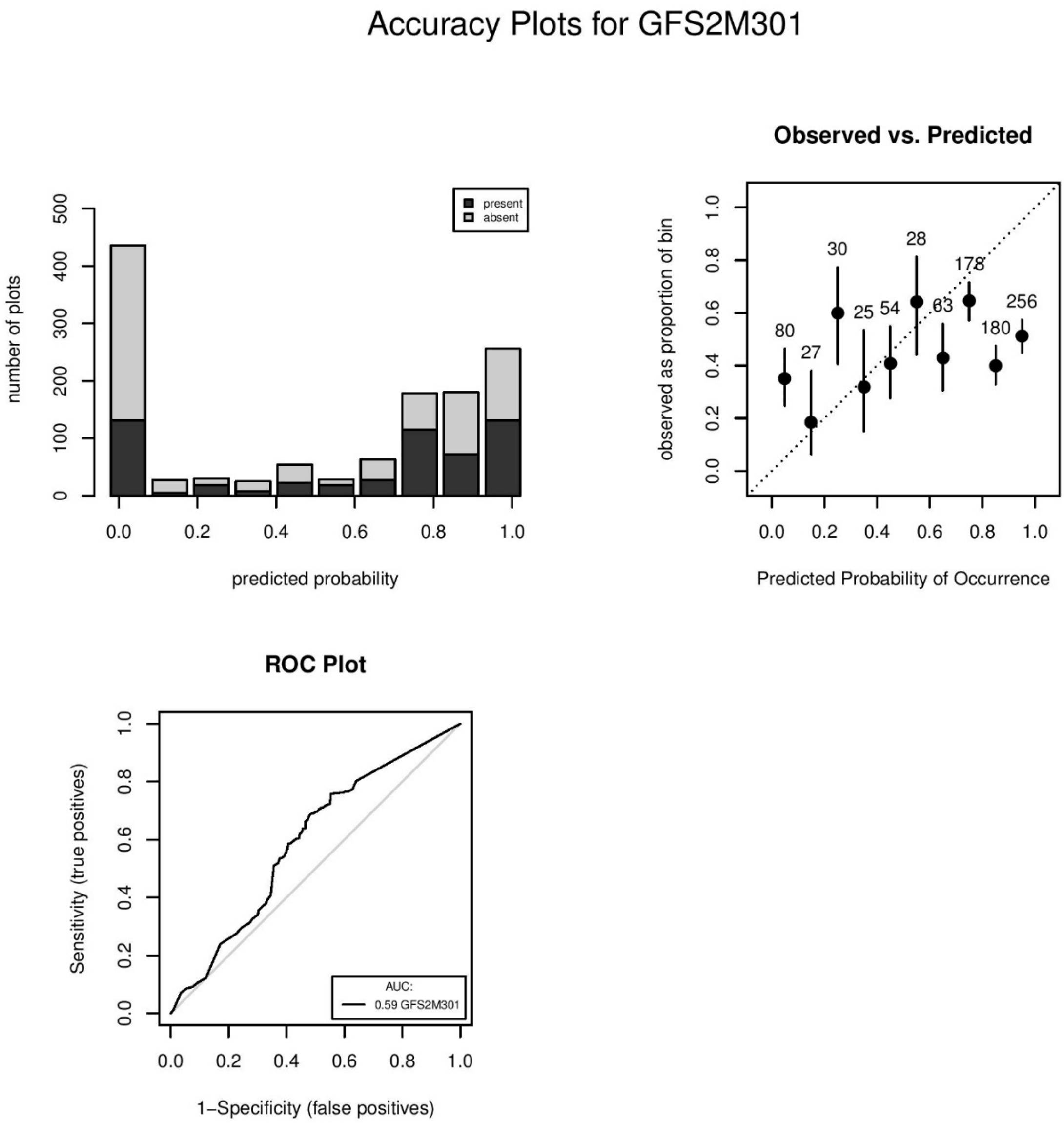
Accuracy Plots for GFS2M245



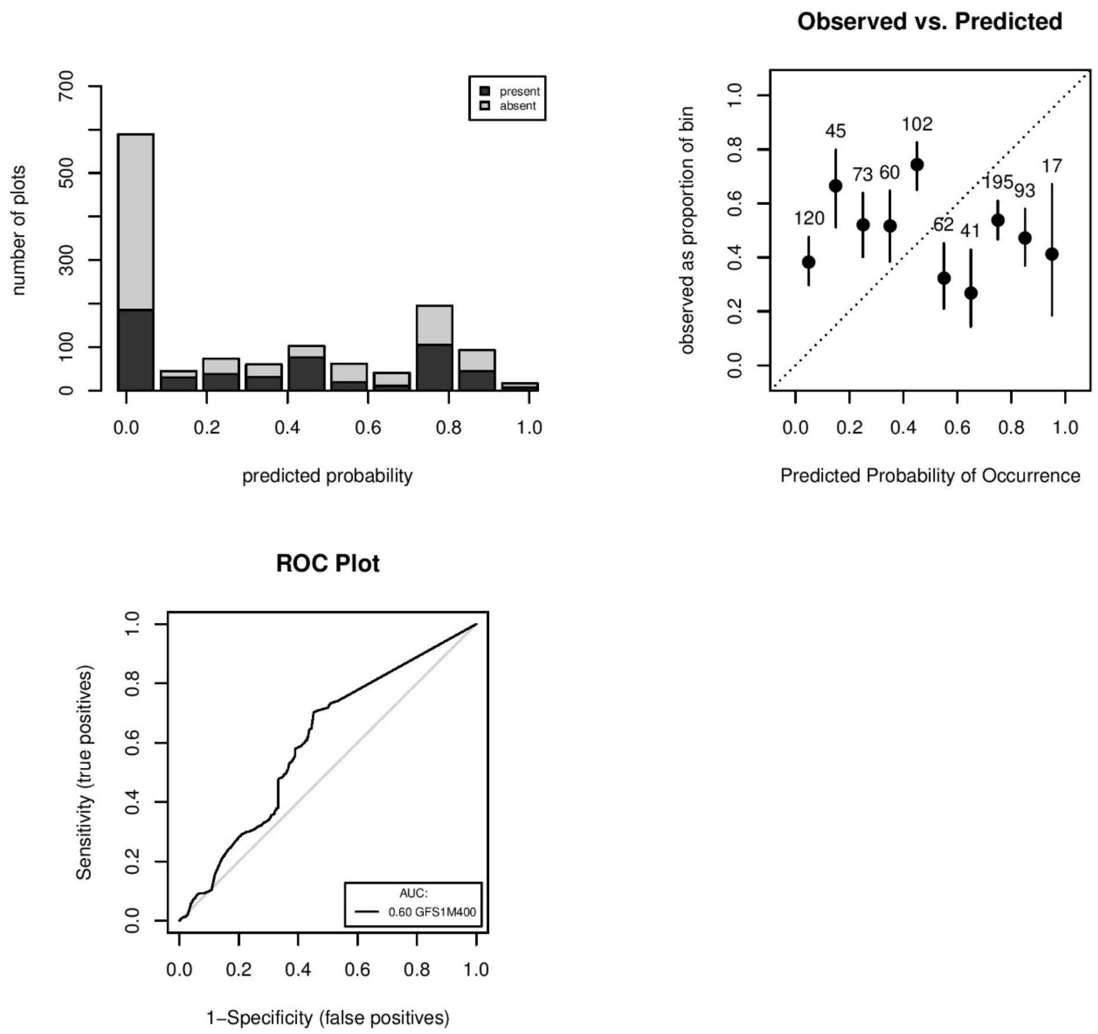

Accuracy Plots for GFS2M300
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
79
22
31
29
51
28
65
162
178
276
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M300

Accuracy Plots for GFS2M300_2

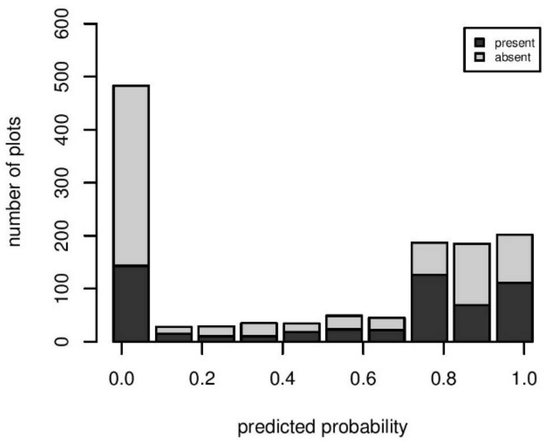


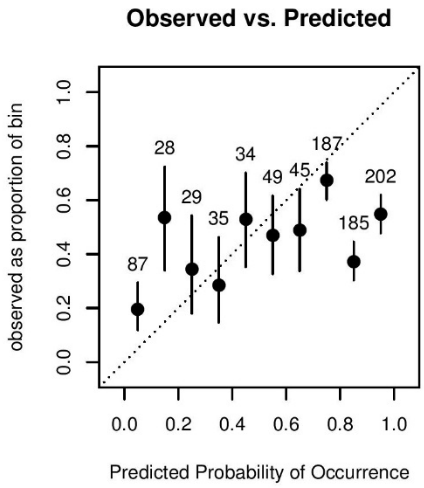

Accuracy Plots for GFS2M301
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
80
27
30
25
54
28
63
178
180
256
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.59 GFS2M301

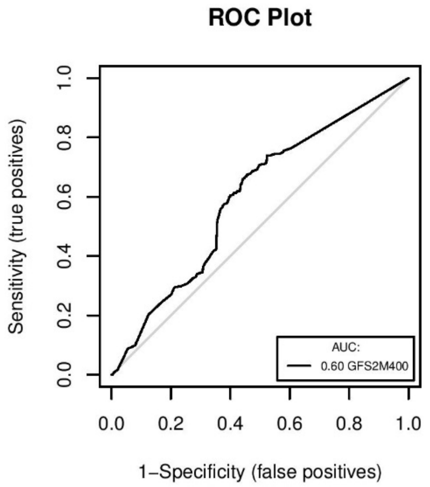
Accuracy Plots for GFS1M400

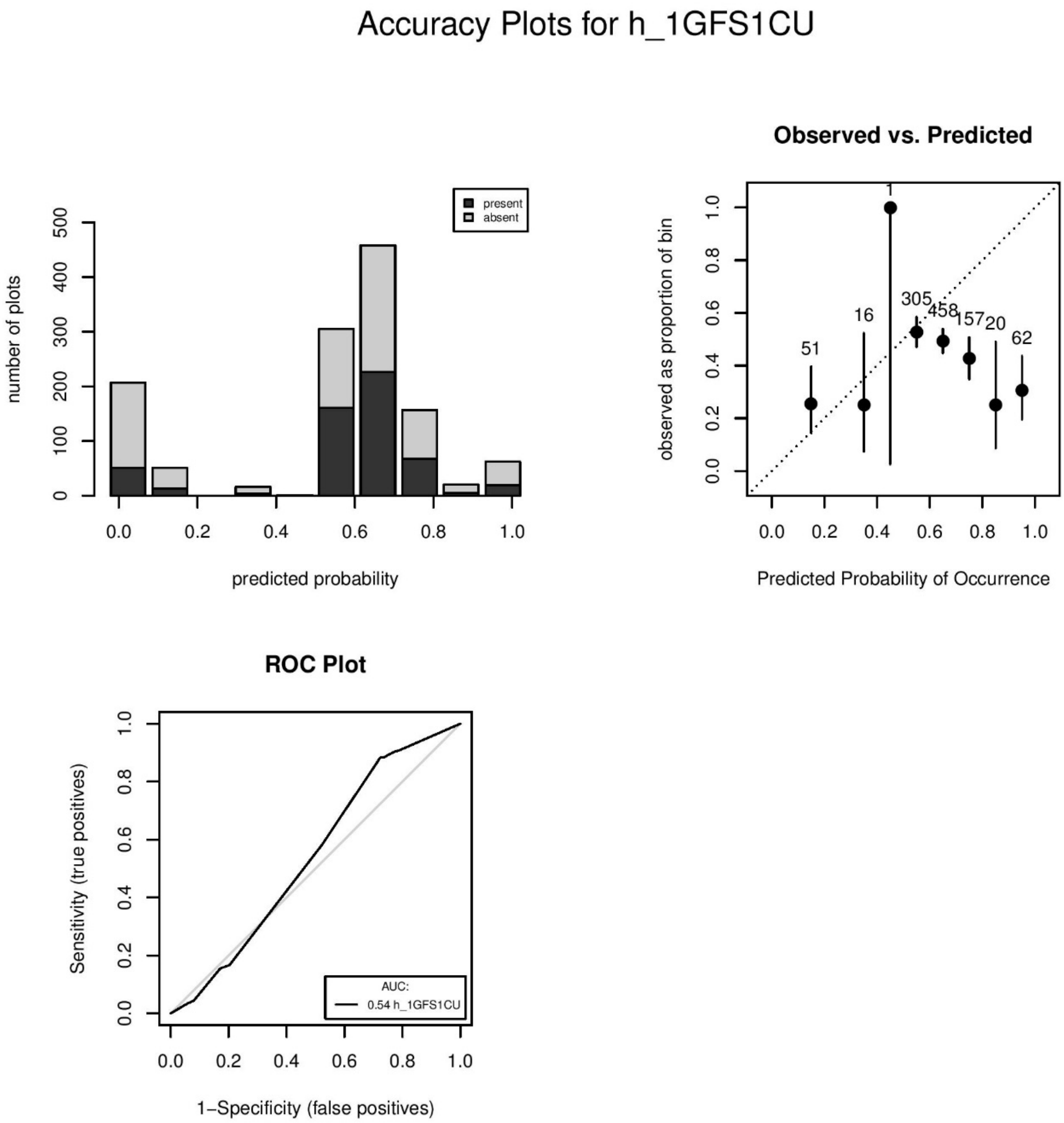


Accuracy Plots for GFS2M400

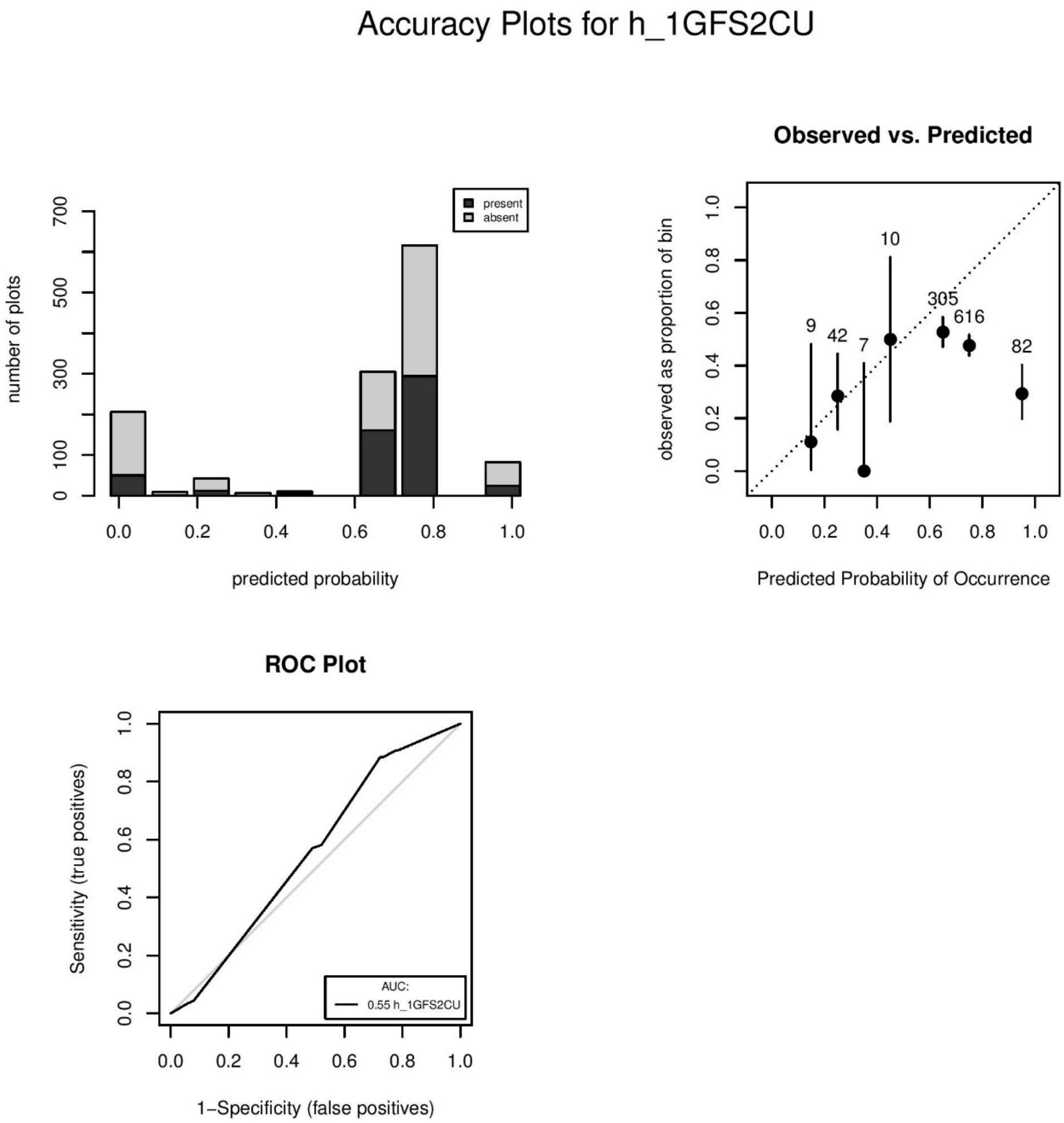


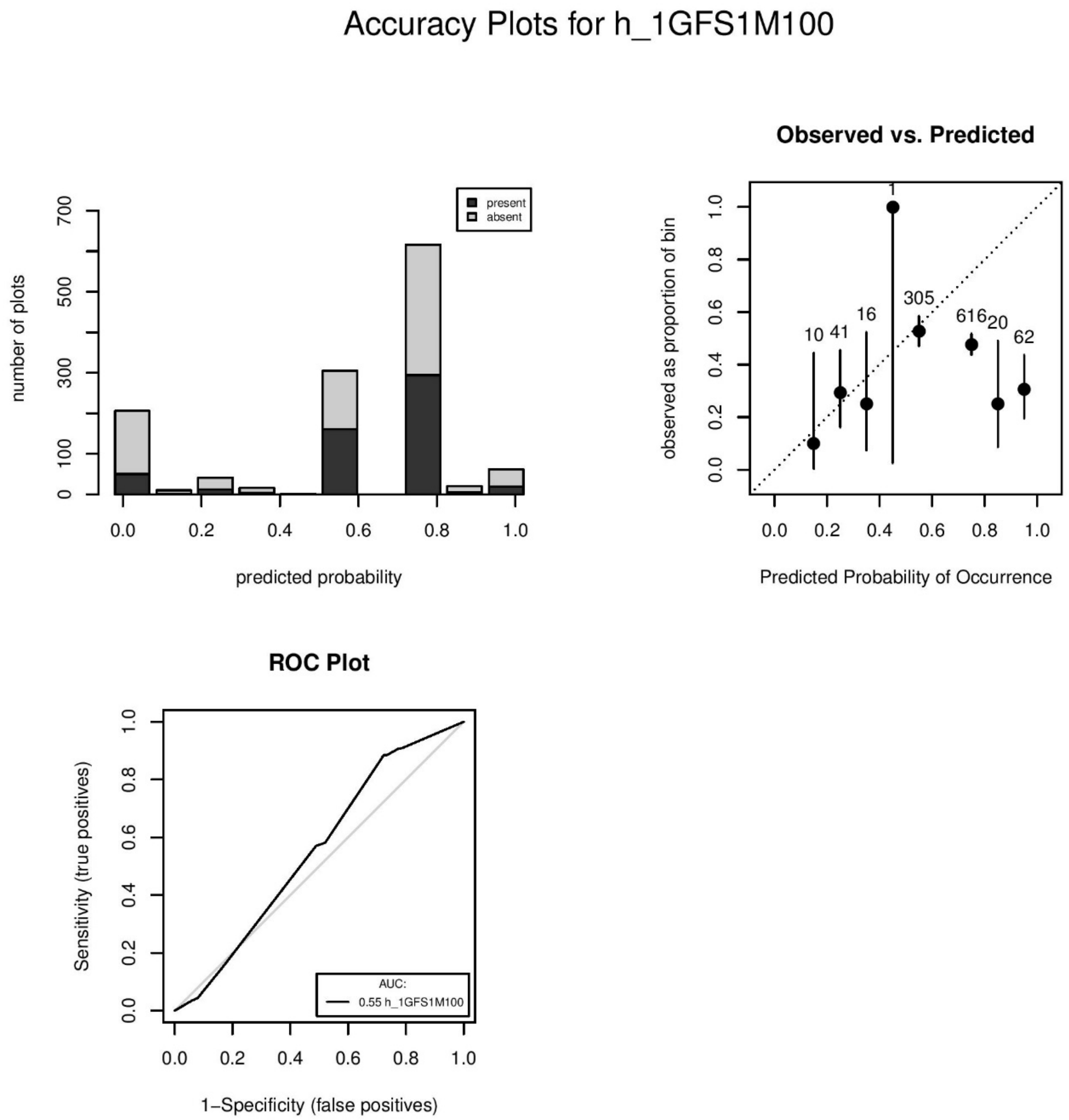


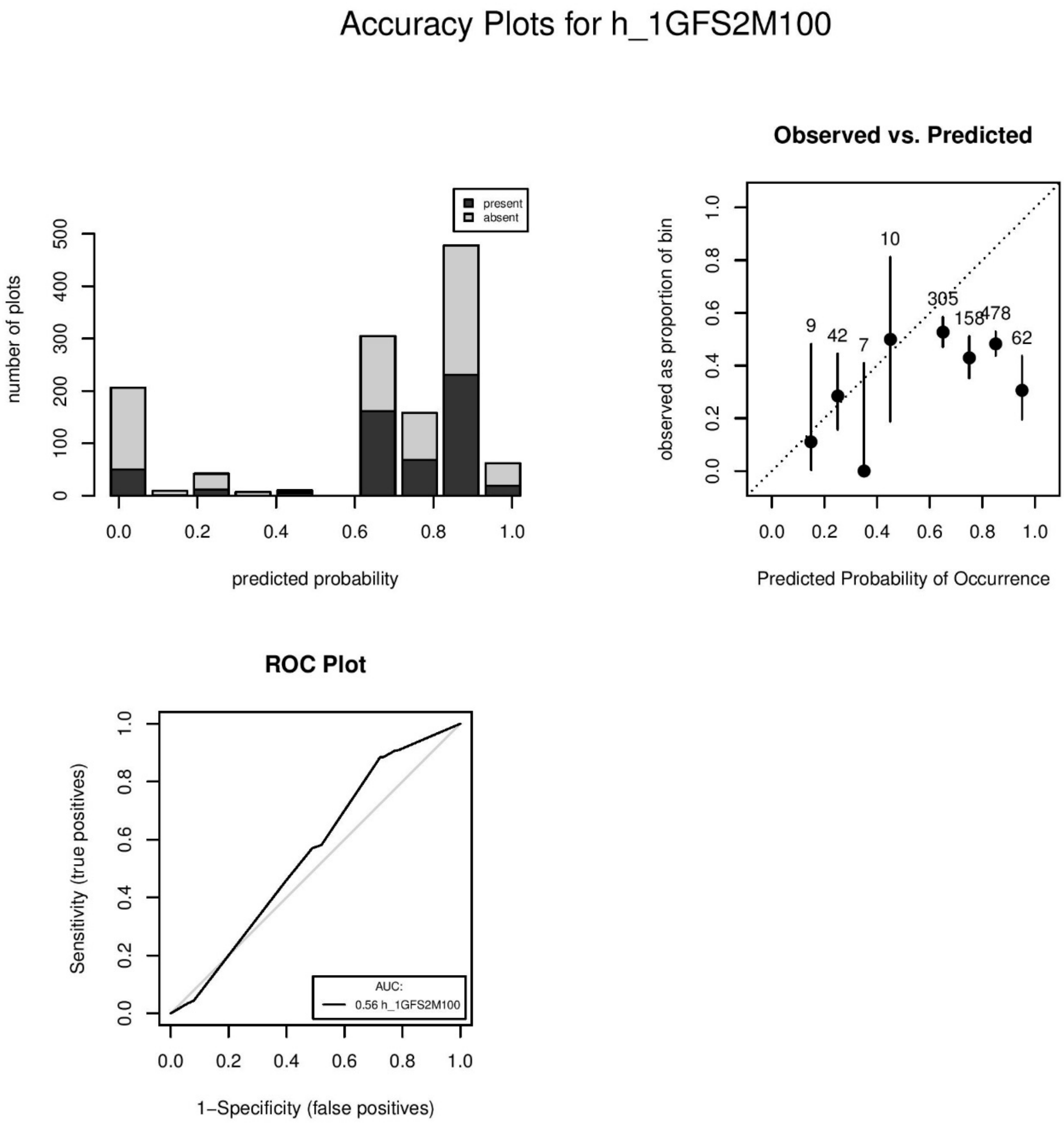


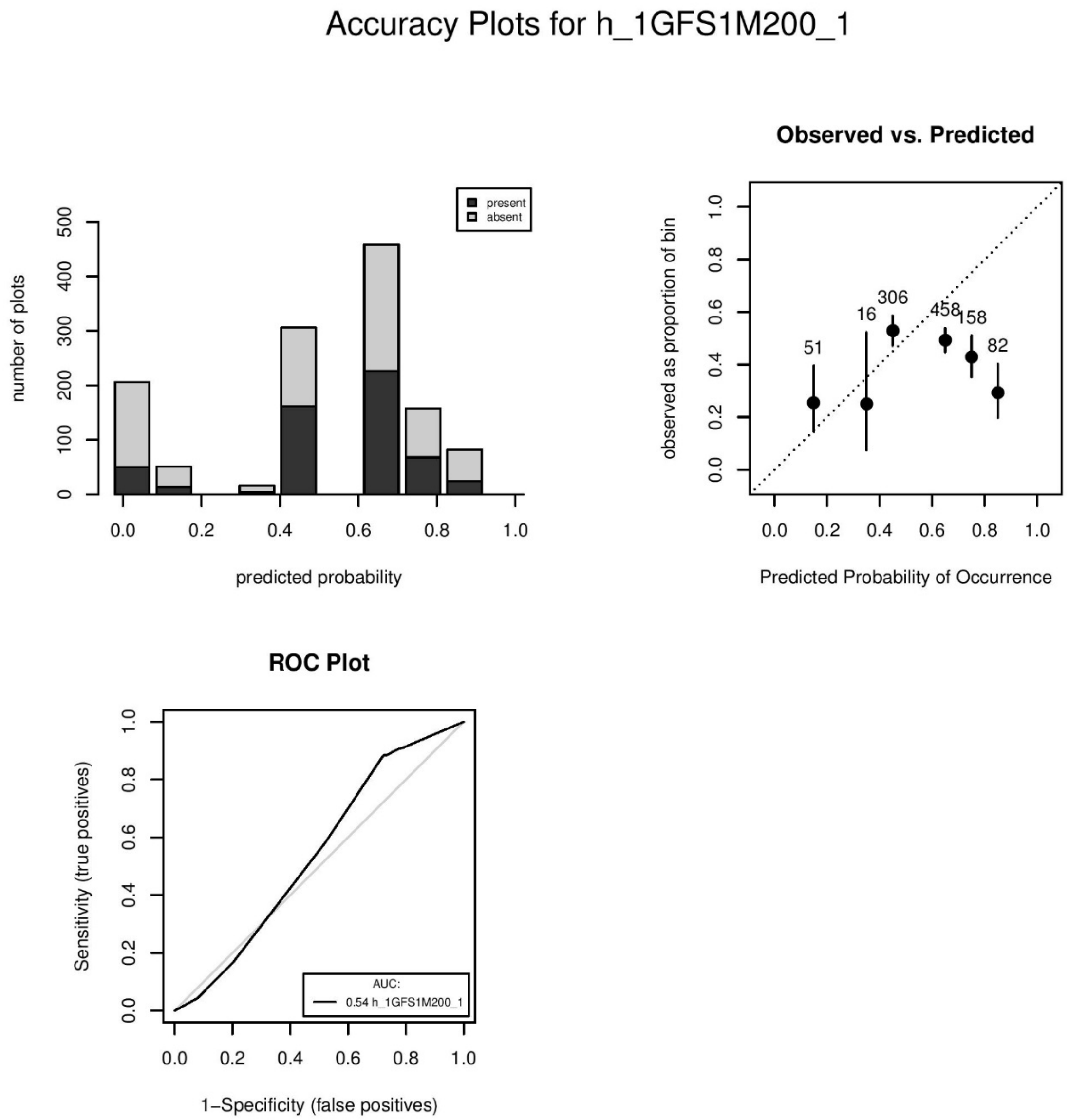


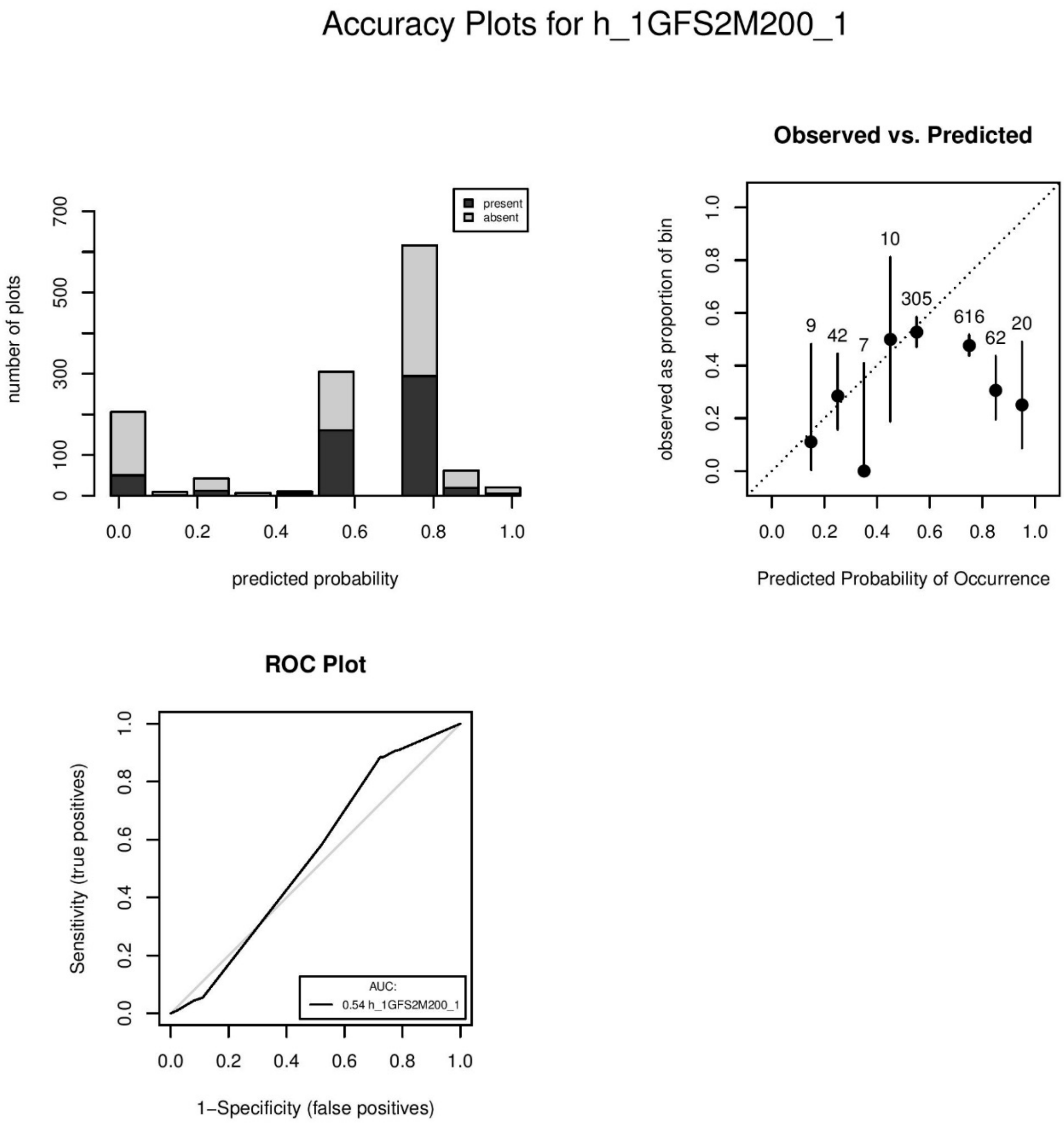
Accuracy Plots for h_1GFS1CU
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
1
16
51
305
458
157
20
62
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.54 h_1GFS1CU

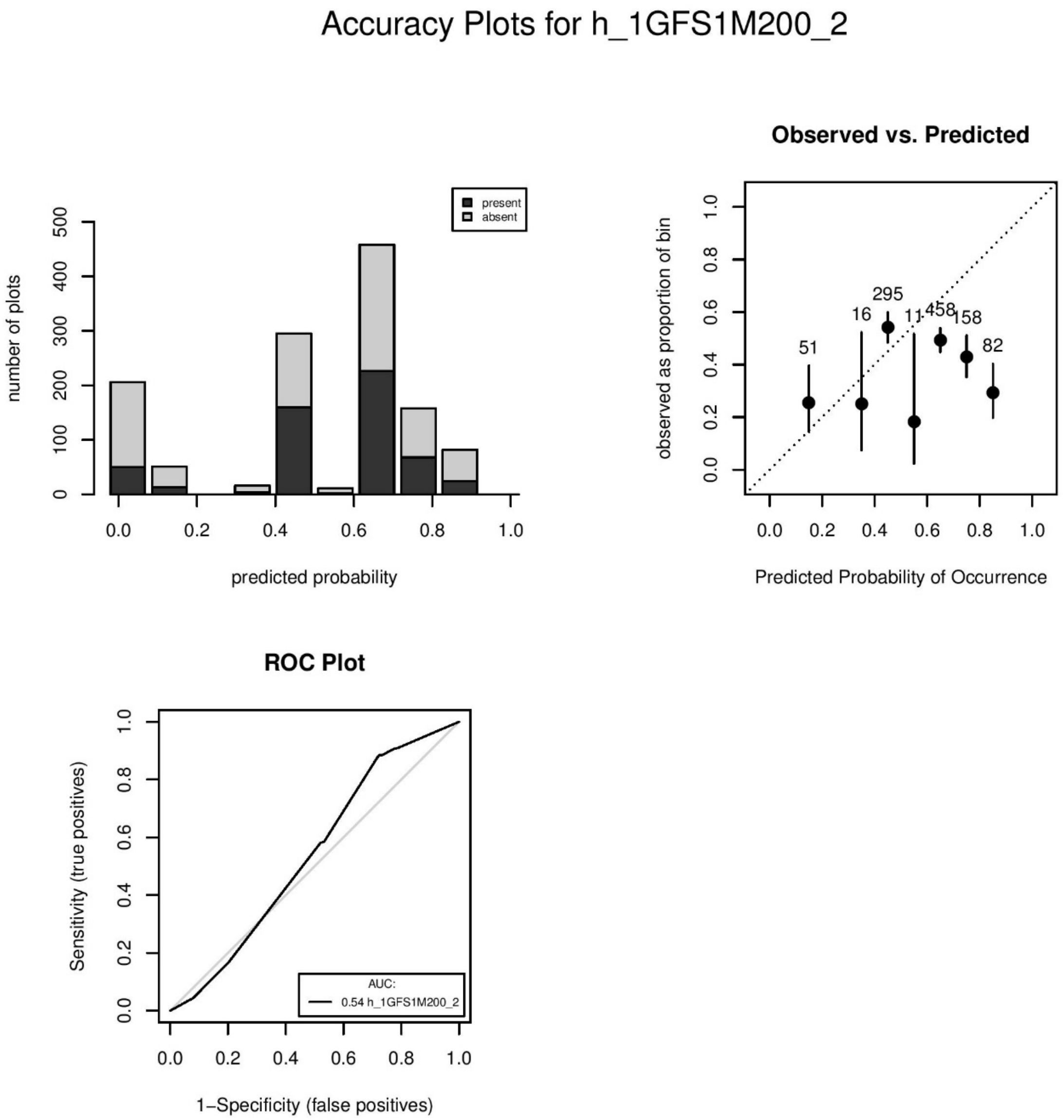

Accuracy Plots for h_1GFS2CU
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
305
616
82
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.55 h_1GFS2CU

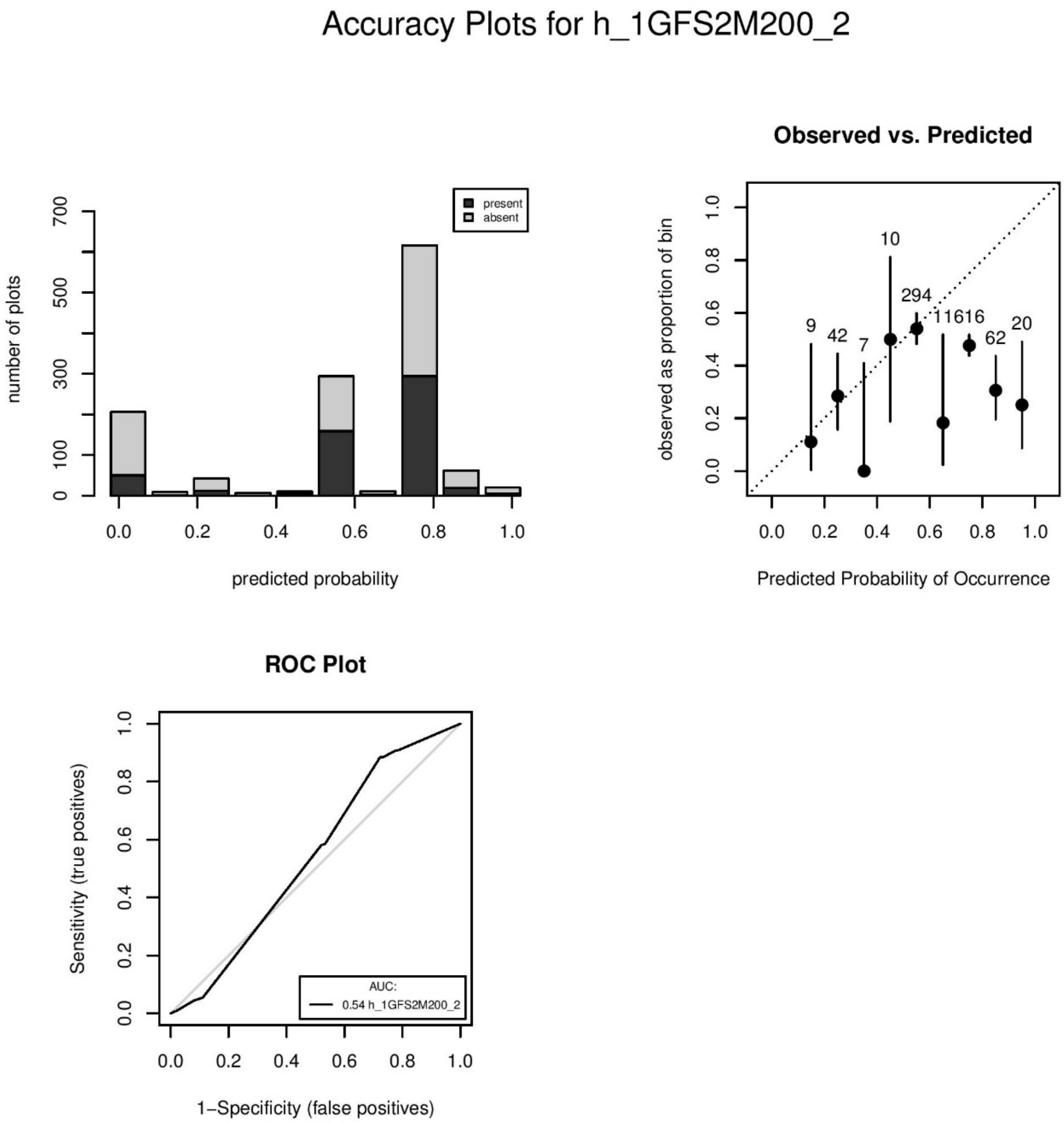

Accuracy Plots for h_1GFS1M100
present
absent
number of plots
0
100
300
500
700
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
10
41
16
1
305
616
20
62
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.55 h_1GFS1M100

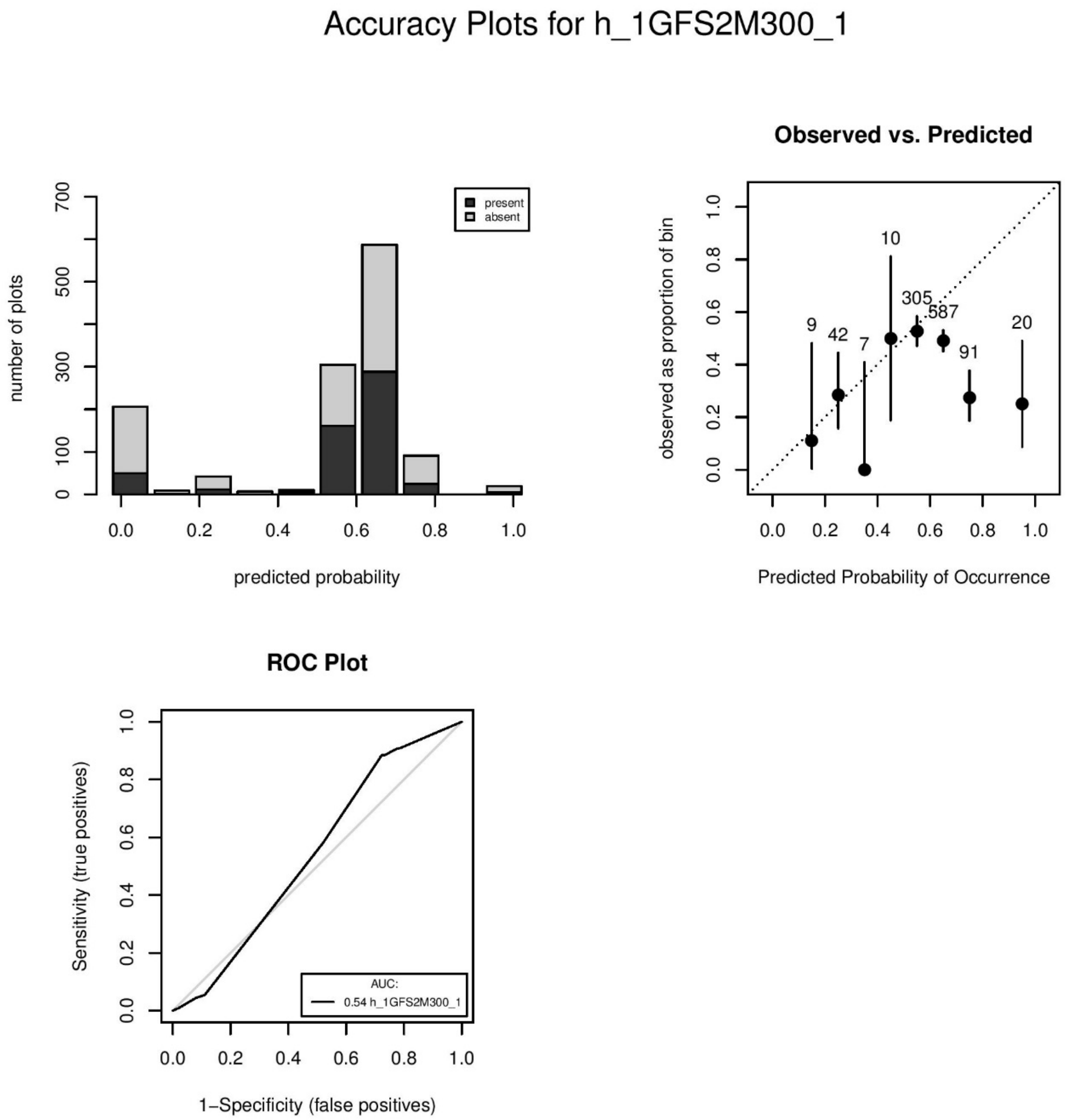

Accuracy Plots for h_1GFS2M100
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
305
158
478
62
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.56 h_1GFS2M100


Accuracy Plots for h_1GFS1M200_1
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
51
16
306
458
158
82
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.54 h_1GFS1M200_1

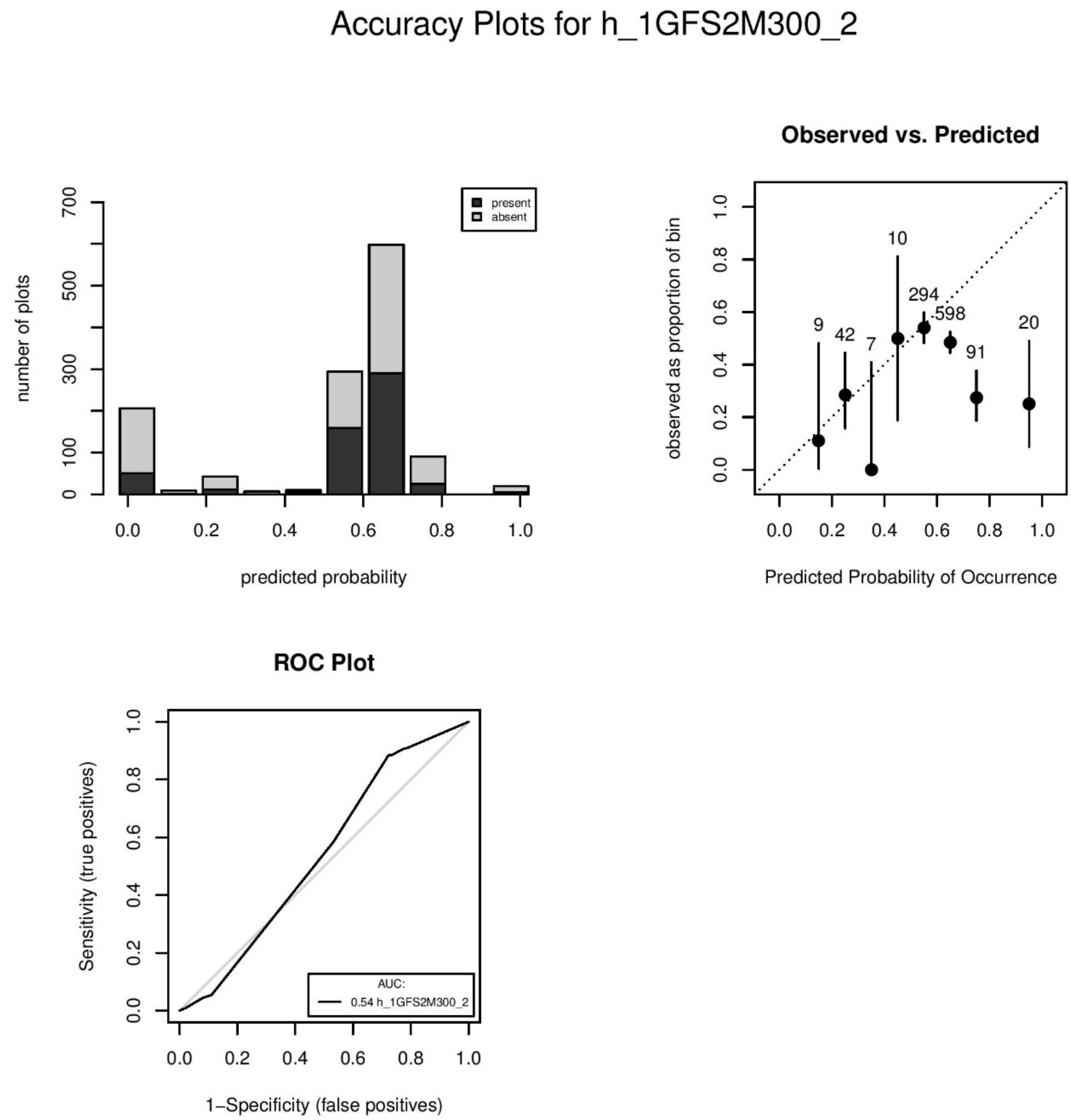

Accuracy Plots for h_1GFS2M200_1
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
305
616
62
20
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.54 h_1GFS2M200_1


Accuracy Plots for h_1GFS1M200_2
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
51
16
295
11
458
158
82
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.54 h_1GFS1M200_2


Accuracy Plots for h_1GFS2M200_2
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
294
11616
62
20
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.54 h_1GFS2M200_2

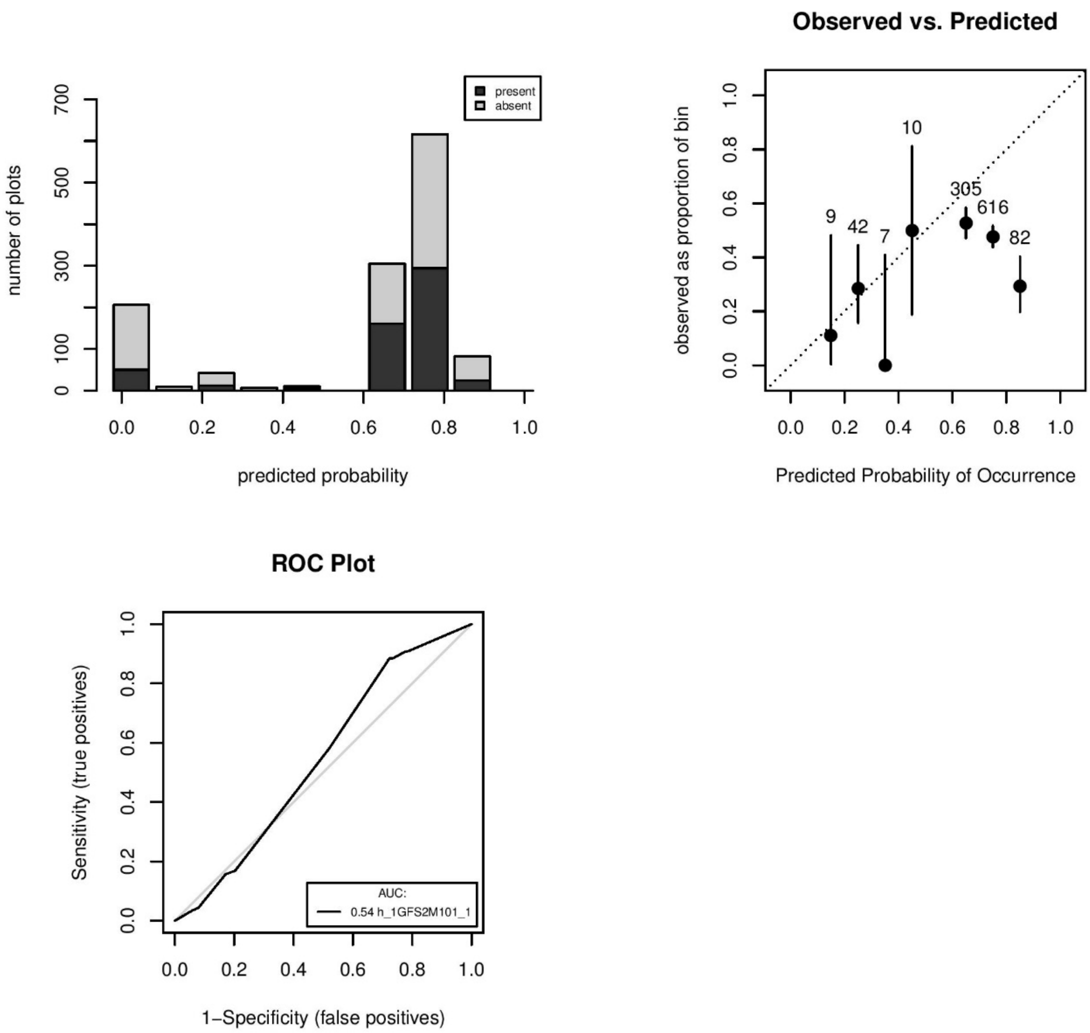


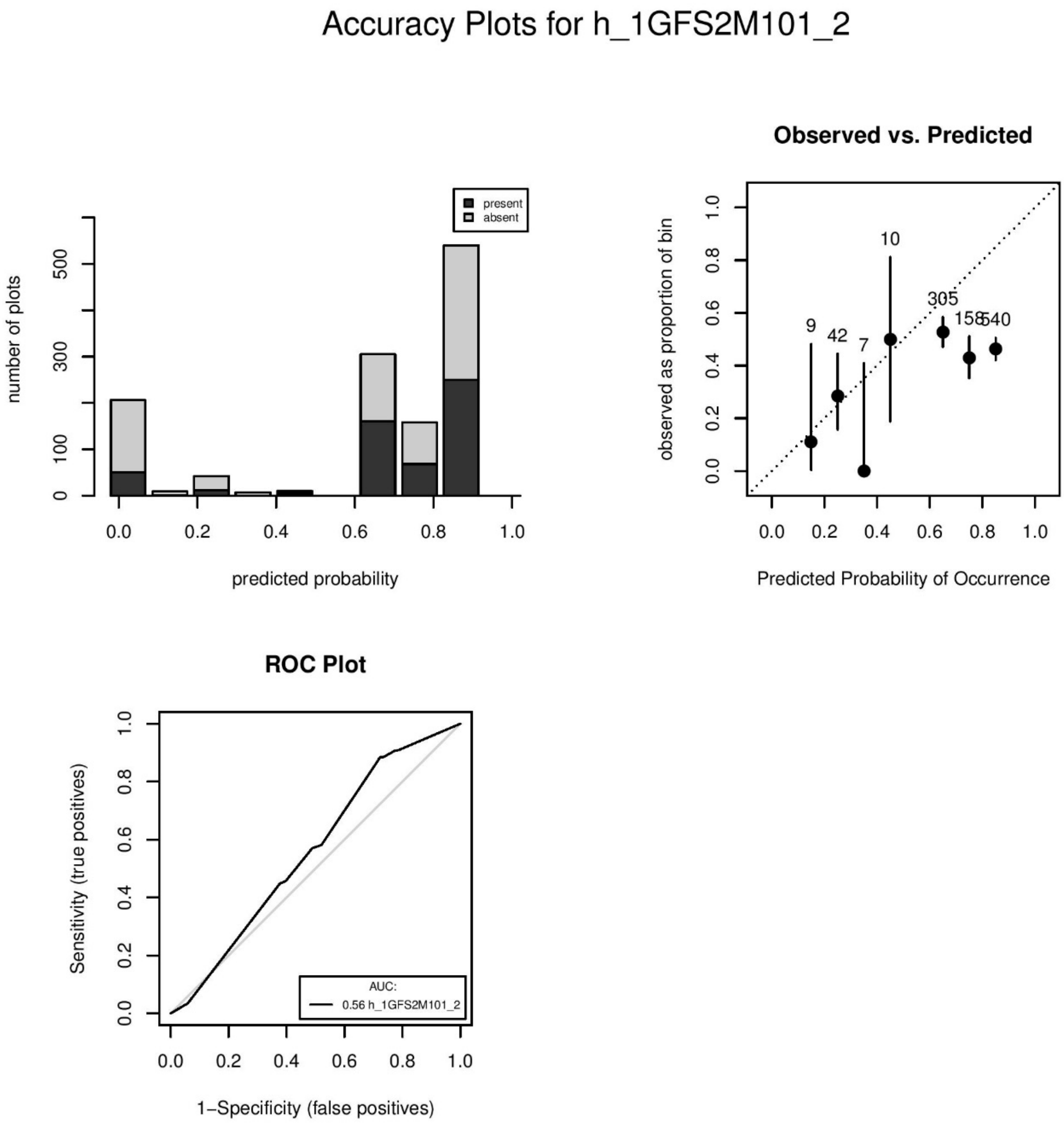
Accuracy Plots for h_1GFS2M300_1
number of plots
predicted probability
present
absent
0
100
300
500
700
0.0
0.2
0.4
0.6
0.8
1.0
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
305
587
91
20
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.54 h_1GFS2M300_1

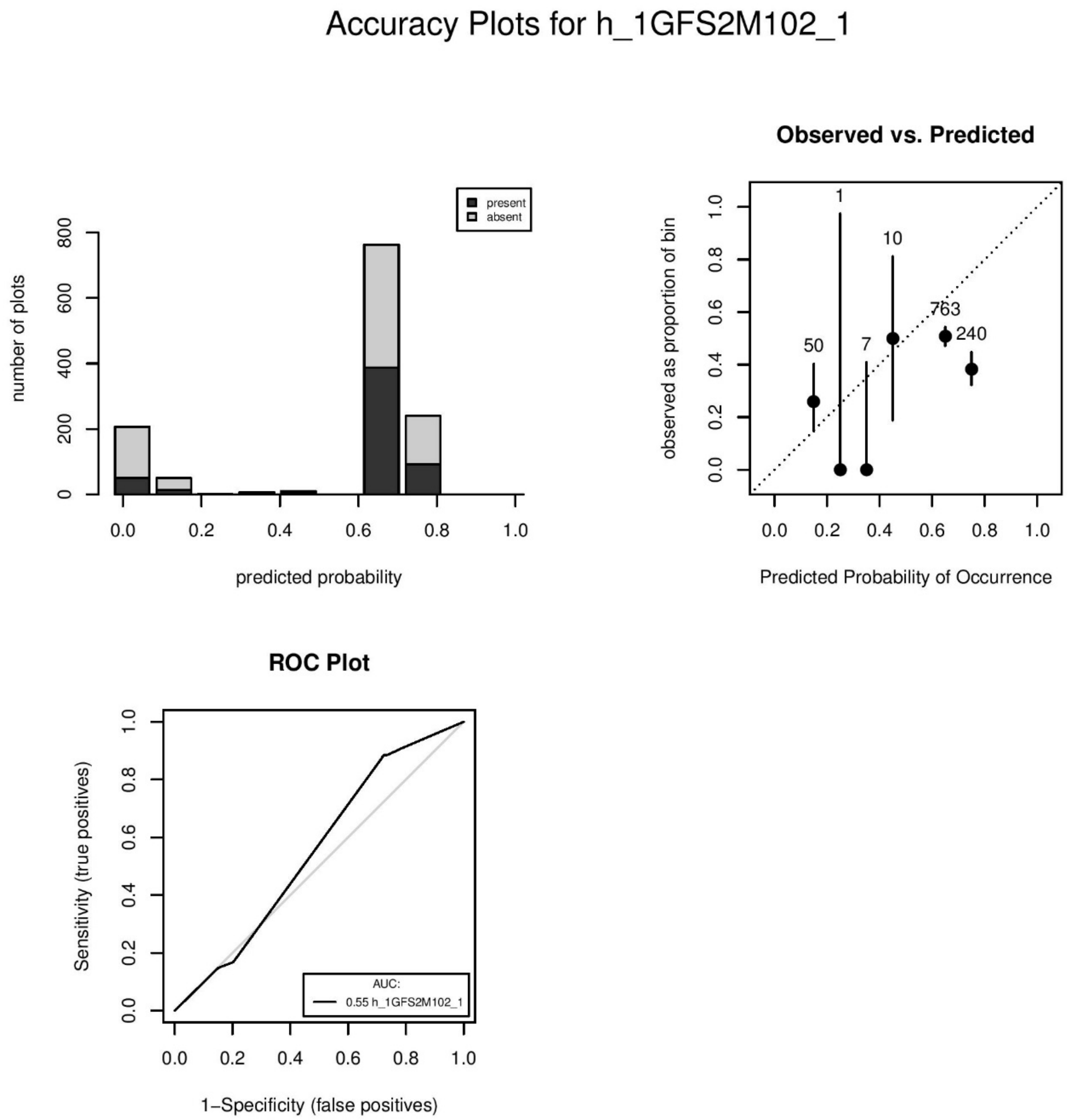


Accuracy Plots for h_1GFS2M300_2
present
absent
number of plots
0
100
300
500
700
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
294
598
91
20
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.54 h_1GFS2M300_2

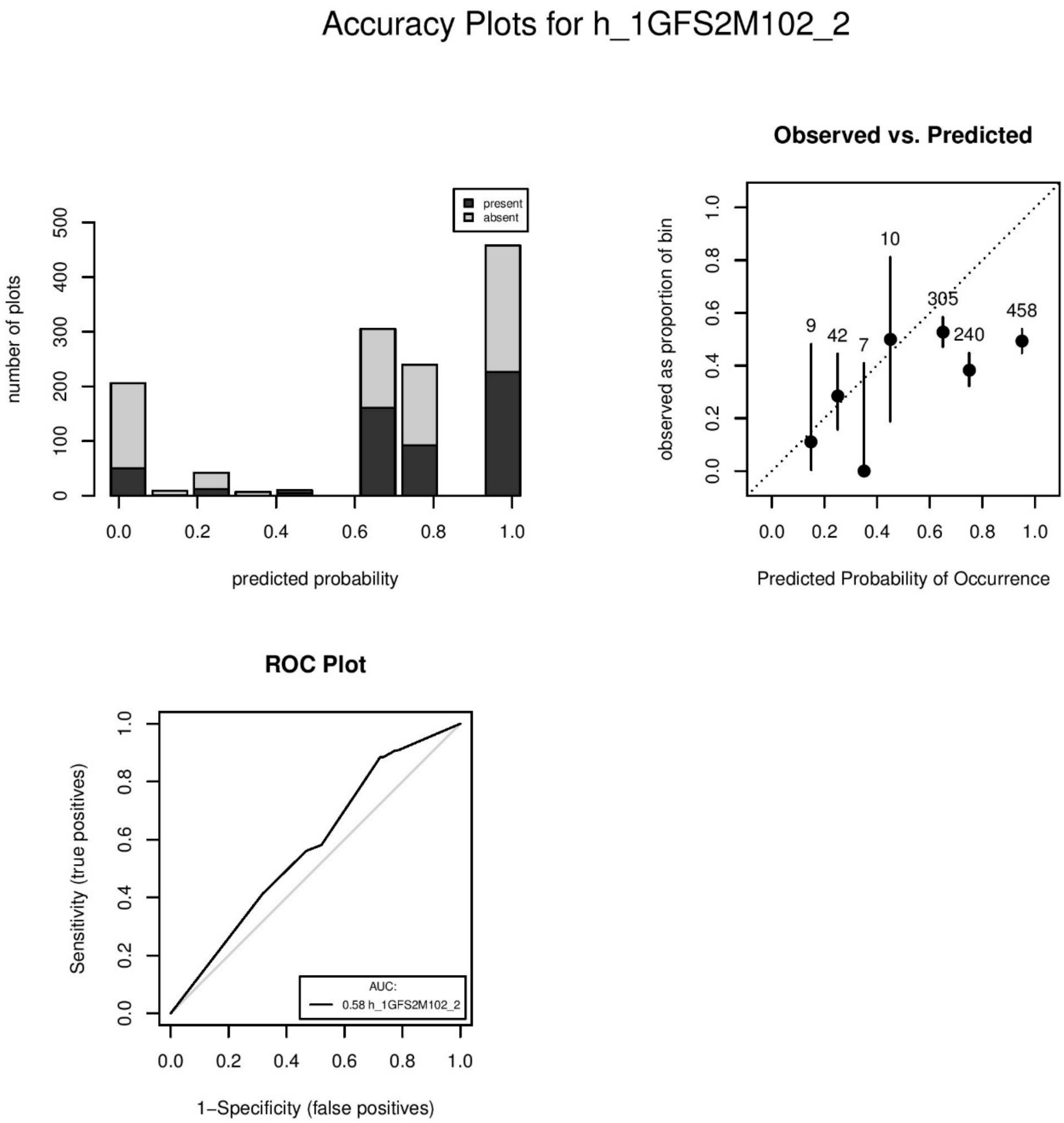
Accuracy Plots for h_1GFS2M101_1

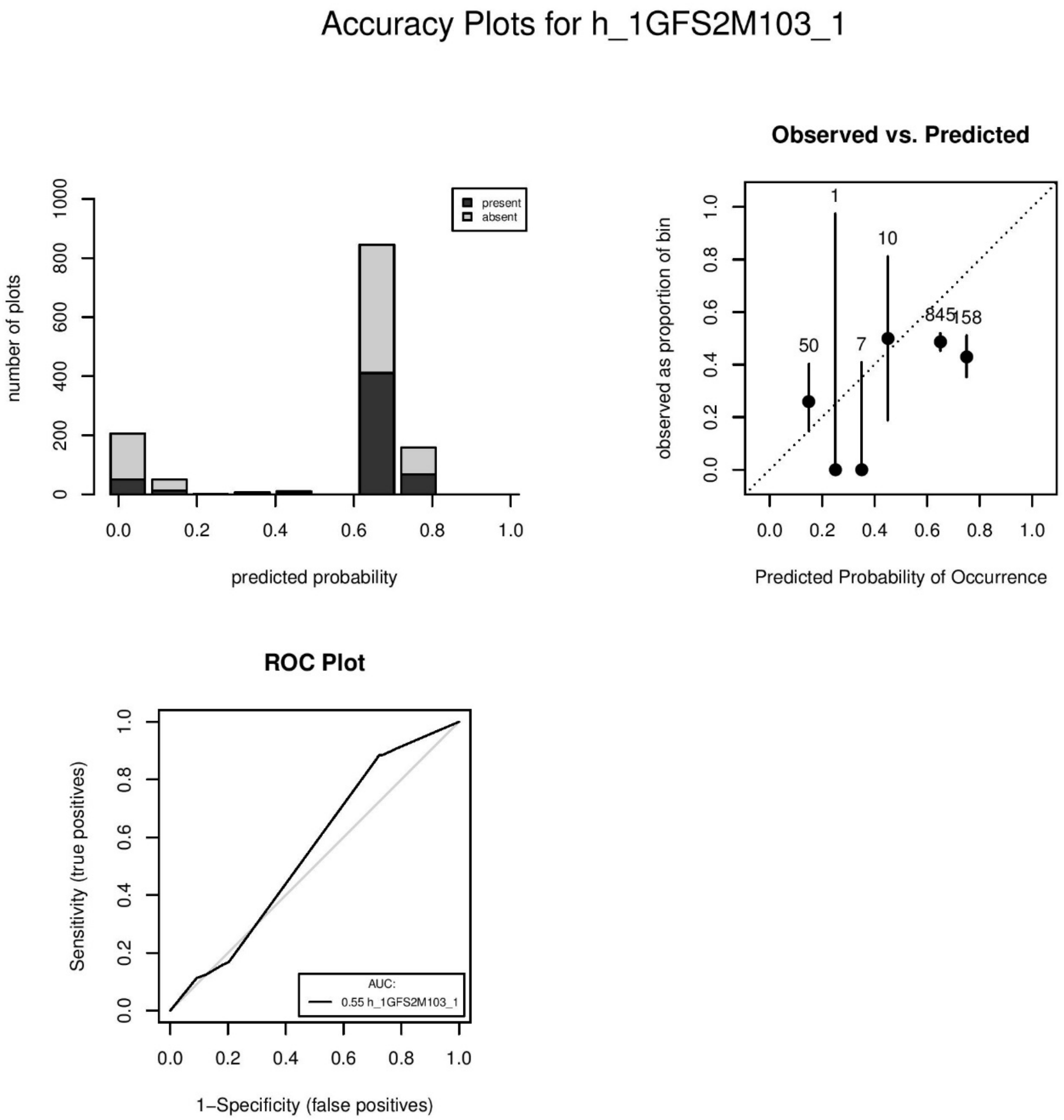


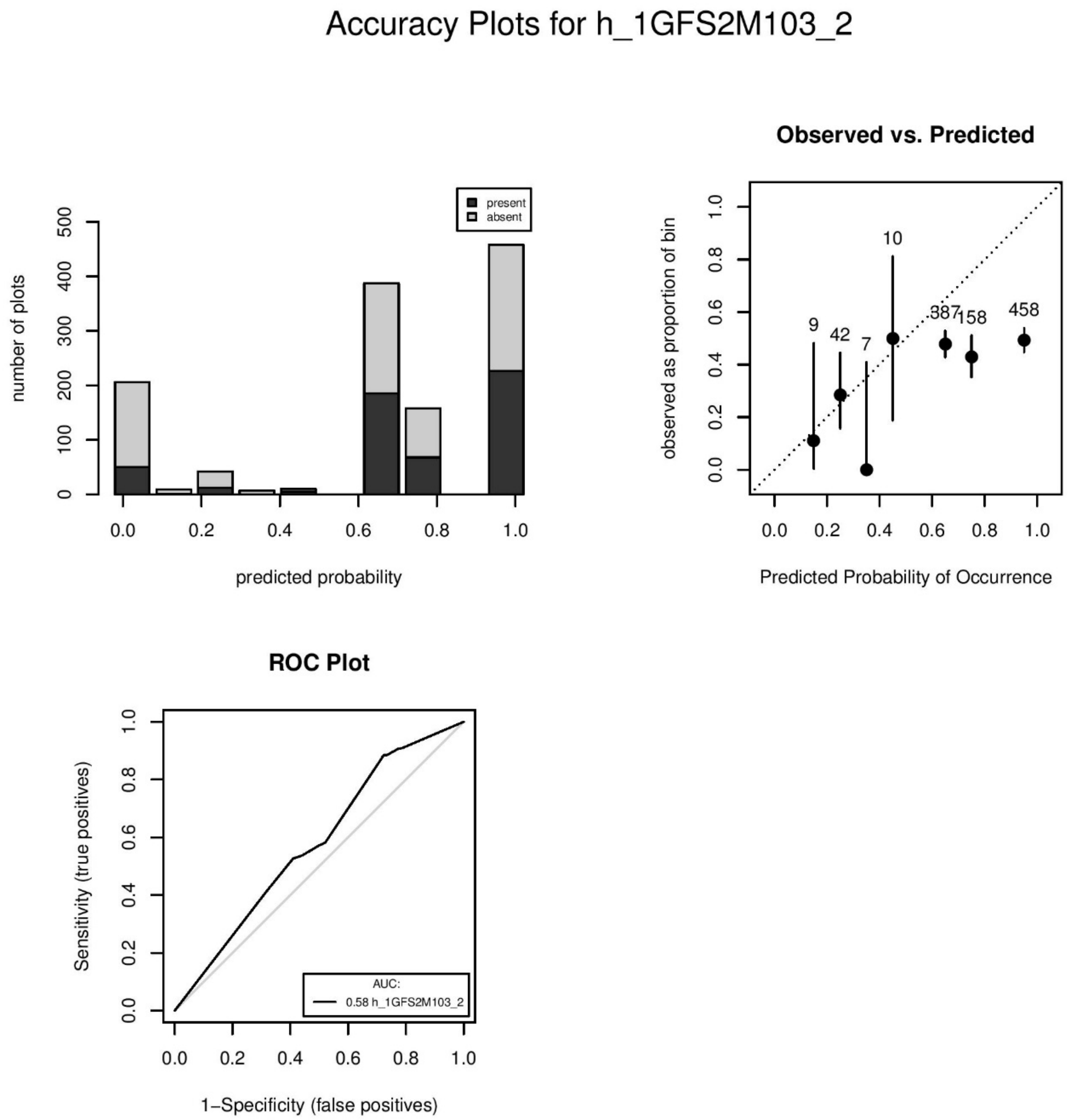

Accuracy Plots for h_1GFS2M101_2
Observed vs. Predicted
present
absent
number of plots
predicted probability
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
305
158
540
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.56 h_1GFS2M101_2

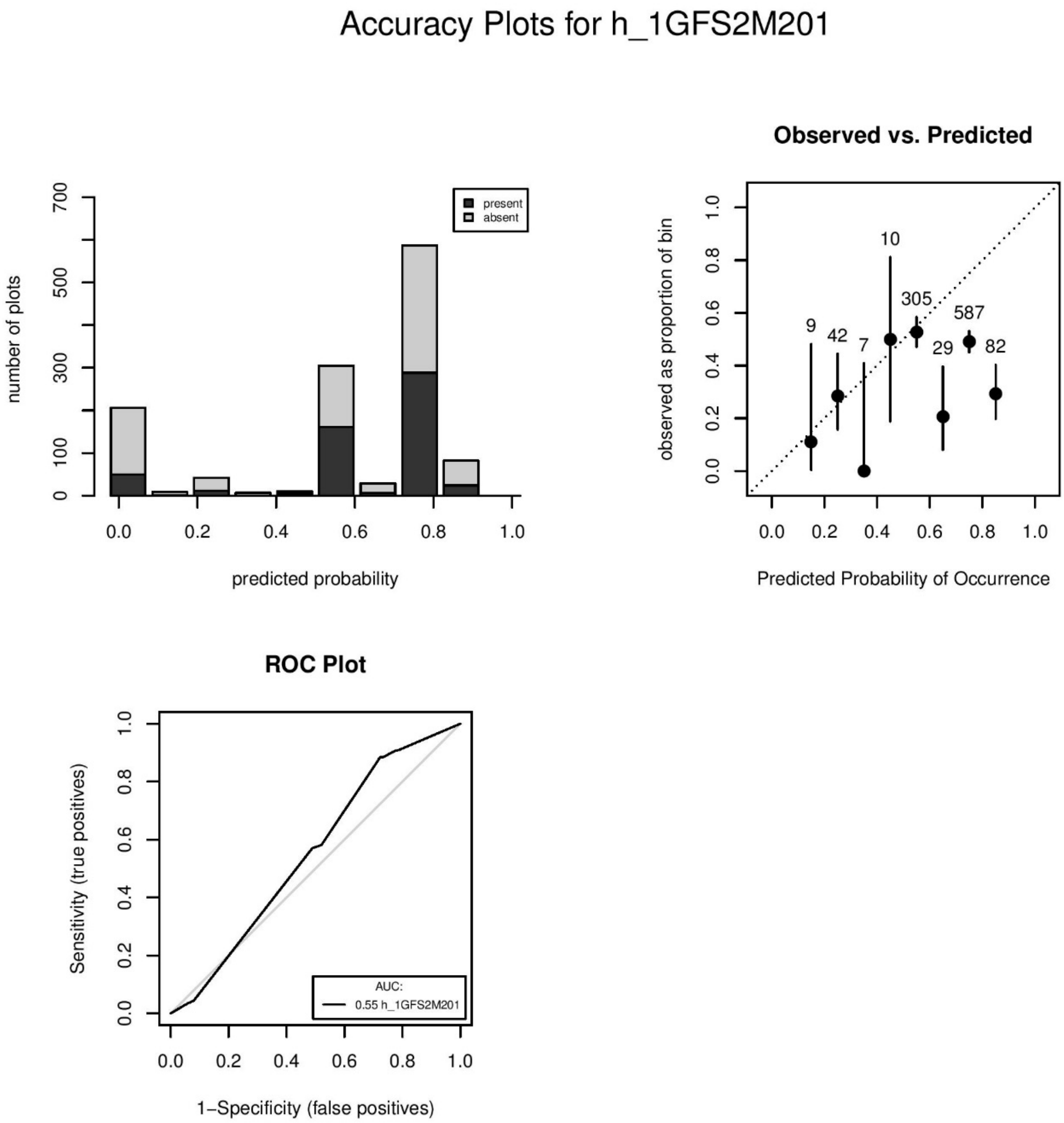


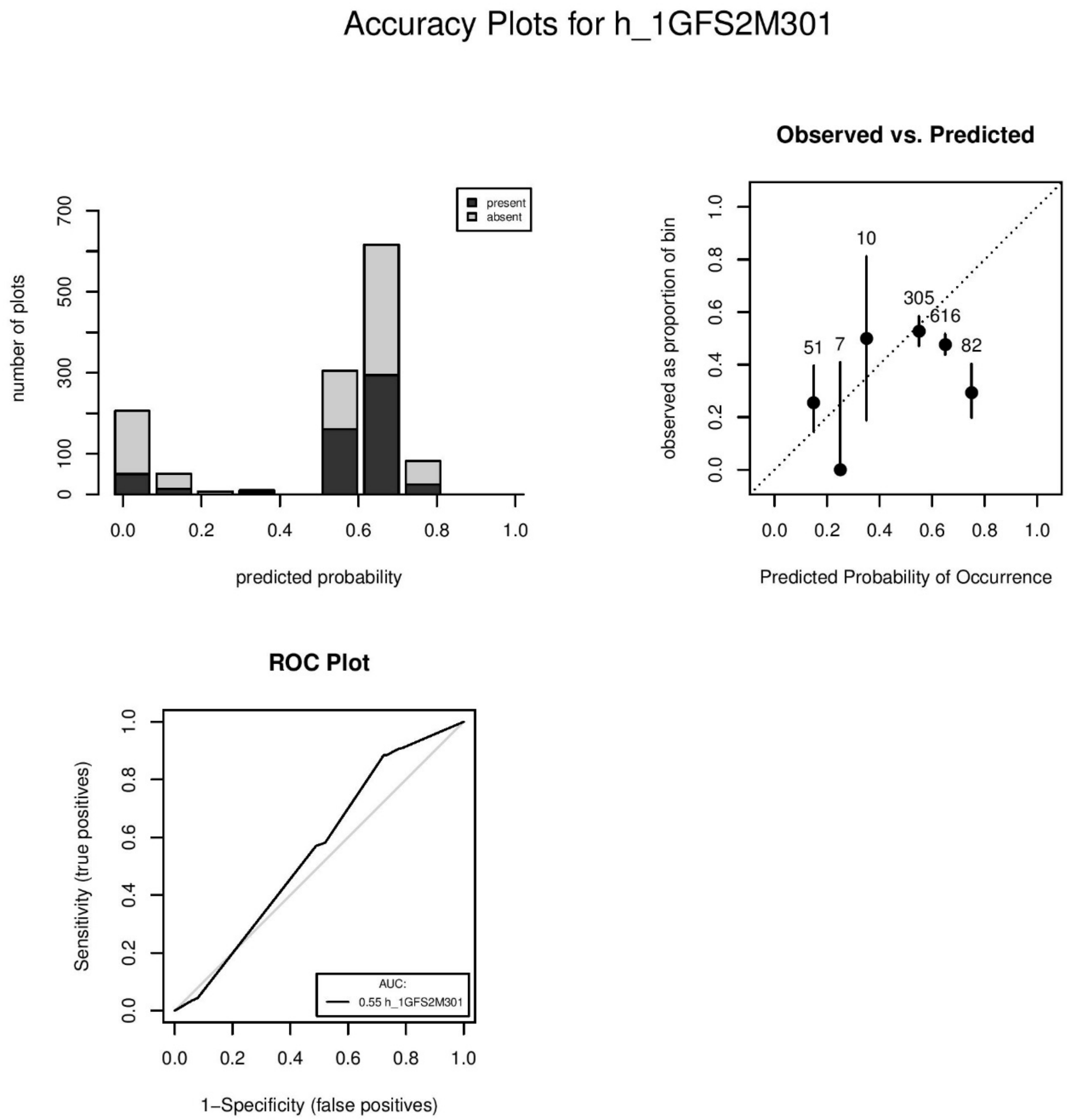
Accuracy Plots for h_1GFS2M102_1
present
absent
number of plots
0
200
400
600
800
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
1
10
763
240
50
7
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
AUC:
0.55 h_1GFS2M102_1
1−Specificity (false positives)

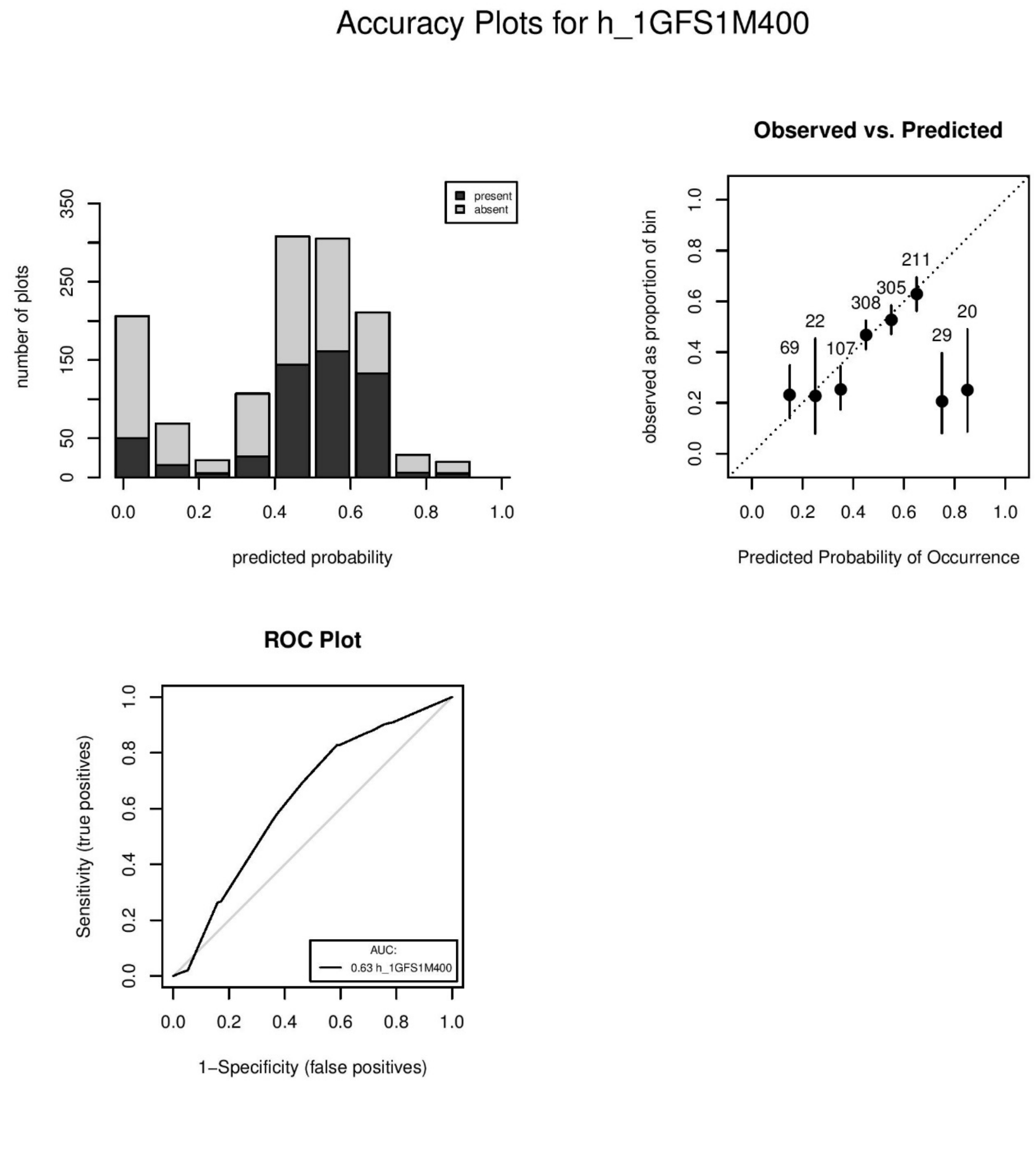

Accuracy Plots for h_1GFS2M102_2
present
absent
number of plots
0
100
200
300
400
500
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
305
240
458
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 h_1GFS2M102_2


Accuracy Plots for h_1GFS2M103_1
number of plots
predicted probability
present
absent
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
50
1
7
10
845
158
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.55 h_1GFS2M103_1


Accuracy Plots for h_1GFS2M103_2
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
387
158
458
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.58 h_1GFS2M103_2


Accuracy Plots for h_1GFS2M201
present
absent
number of plots
predicted probability
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
9
42
7
10
305
29
587
82
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.55 h_1GFS2M201


Accuracy Plots for h_1GFS2M301
present
absent
number of plots
0
100
300
500
700
0.0
0.2
0.4
0.6
0.8
1.0
predicted probability
Observed vs. Predicted
observed as proportion of bin
0.0
0.2
0.4
0.6
0.8
1.0
10
305
616
51
7
82
0.0
0.2
0.4
0.6
0.8
1.0
Predicted Probability of Occurrence
ROC Plot
Sensitivity (true positives)
0.0
0.2
0.4
0.6
0.8
1.0
AUC:
0.55 h_1GFS2M301
0.0
0.2
0.4
0.6
0.8
1.0
1−Specificity (false positives)


Accuracy Plots for h_1GFS1M400
number of plots
predicted probability
present
absent
Observed vs. Predicted
observed as proportion of bin
Predicted Probability of Occurrence
69
22
107
308
305
211
29
20
ROC Plot
Sensitivity (true positives)
1−Specificity (false positives)
AUC:
0.63 h_1GFS1M400

Accuracy Plots for h_1GFS2M400

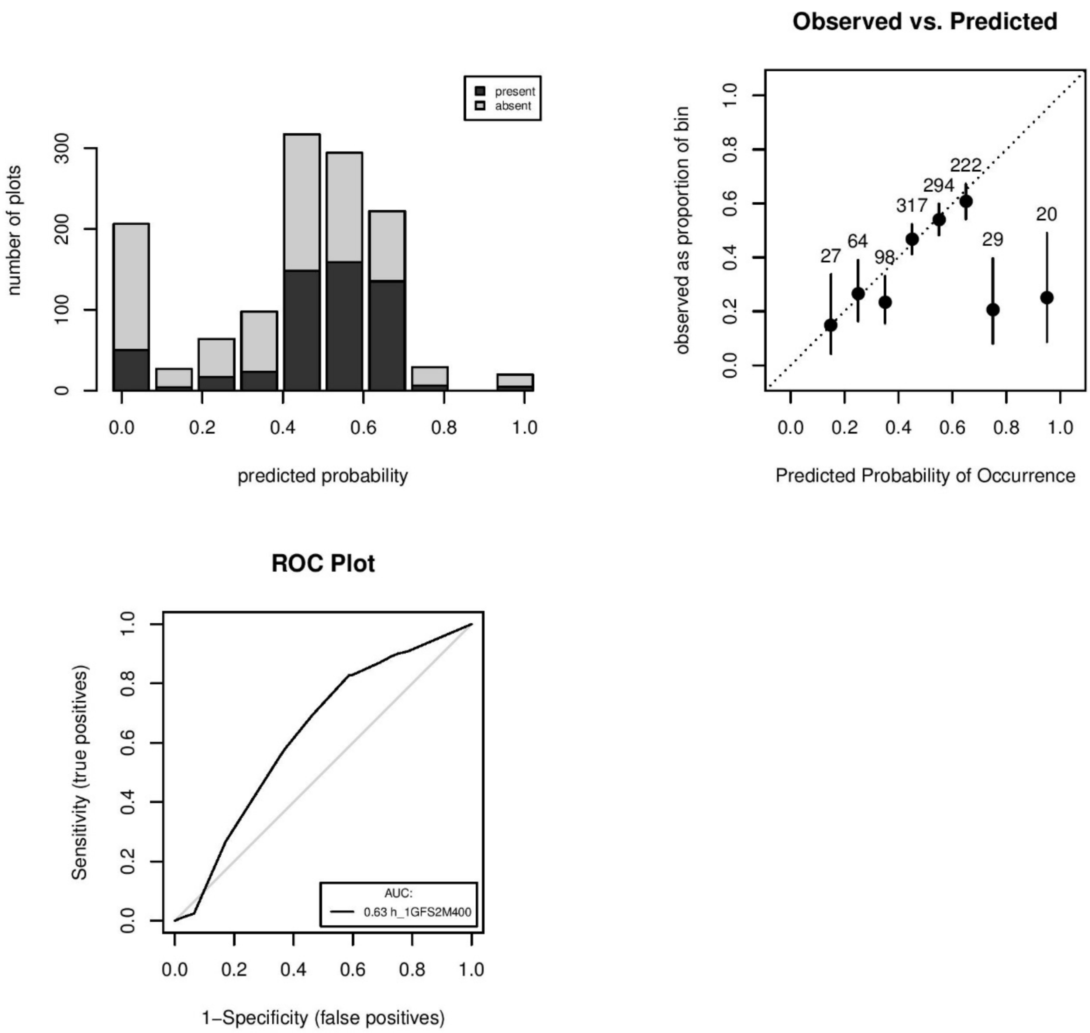
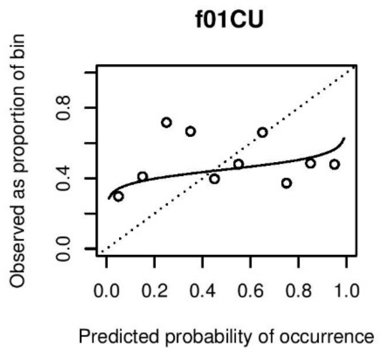
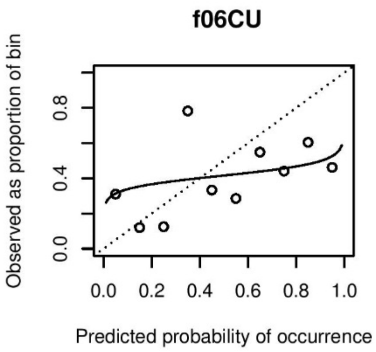
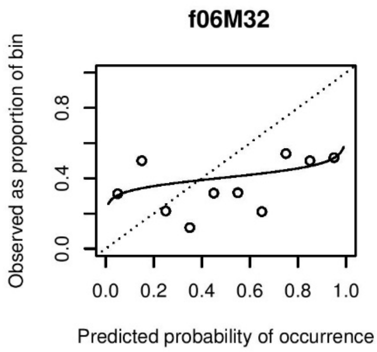
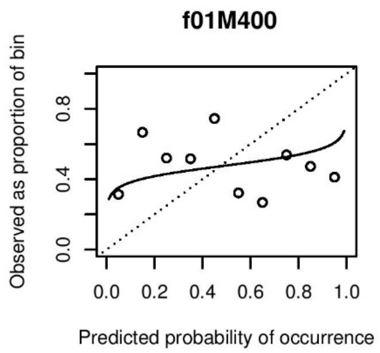


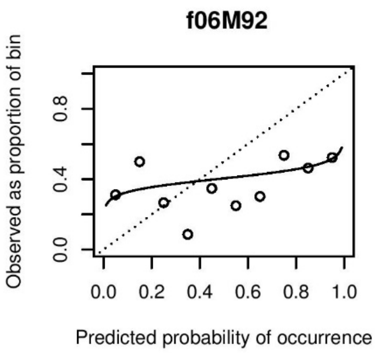
Fig. S5 Regression plots for models with AUC > 0.6 (see Table S5 for details of parameter changes for each model). Solid line is the regression line, which describes the departure from the diagonal dashed line, and represents bias and spread of the model. Models are presented in AUC order, read from top row to bottom row, left to right. The first two plots represent base parameterisation models (CU), followed by alternative parameterisation models. f01 = GFS1 (i.e. 25th percentile values of the group for movement distances and the 25th percentile values for minimum viable habitat area, f06 = GFS2 (i.e. median values for movement distances of the group and 25th percentile values for minimum viable habitat area)

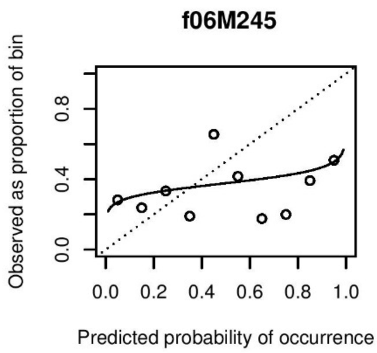

f01CU
Observed as proportion of bin
Predicted probability of occurrence

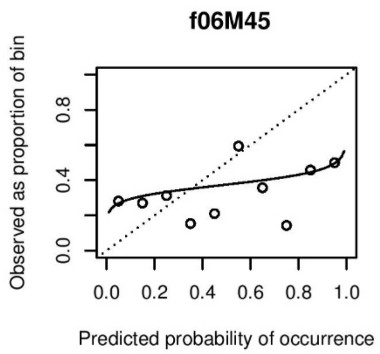

f06CU
Observed as proportion of bin
Predicted probability of occurrence

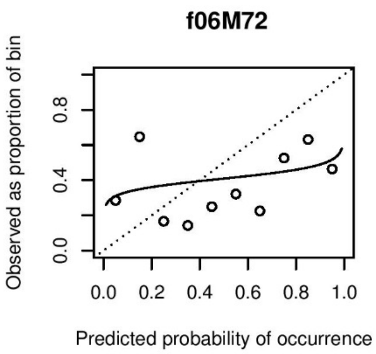

f06M32
Observed as proportion of bin
Predicted probability of occurrence

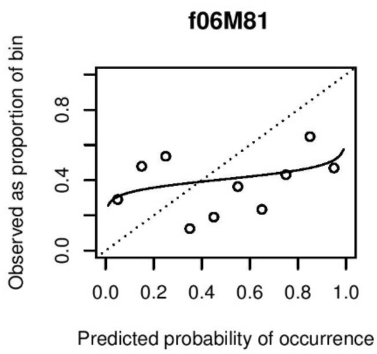

f01M400
Observed as proportion of bin
Predicted probability of occurrence

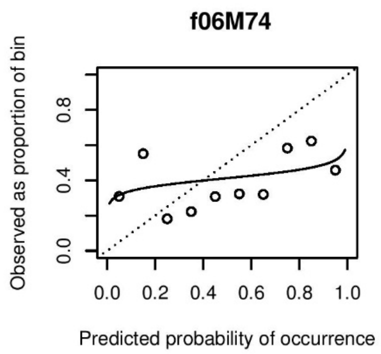

f06M92
Observed as proportion of bin
Predicted probability of occurrence

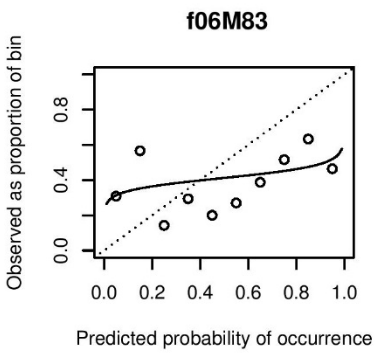

f06M245
Observed as proportion of bin
Predicted probability of occurrence

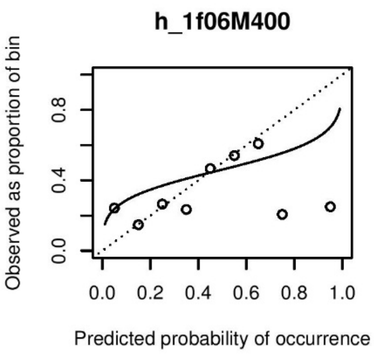

f06M45
Observed as proportion of bin
Predicted probability of occurrence

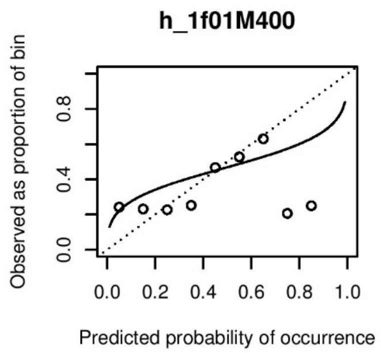

f06M72
Observed as proportion of bin
Predicted probability of occurrence


f06M81
Observed as proportion of bin
Predicted probability of occurrence


f06M74
Observed as proportion of bin
Predicted probability of occurrence


f06M83
Observed as proportion of bin
Predicted probability of occurrence


h_1f06M400
Observed as proportion of bin
Predicted probability of occurrence


h_1f01M400
Observed as proportion of bin
Predicted probability of occurrence

GLOSSARY OF SELECTED TERMS AND CONCEPTS

Terms and concepts in bold have been defined. Definitions and explanations for terms and concepts without a footnote are taken from the relevant chapters.

Term/Concept **(Chapter in which term or concept first described)**	**Definition**	**Additional chapter(s) where term or concept features**
Benefit (Chapter 2)	see **Biodiversity Forecasting Tool** and **Native Vegetation Management Benefit Analysis**	
Broad scale (Chapter 2)	Broad scale (state scale) aligns with the area of the state of New South Wales (i.e. ~10^8 ha), and is important for contextualising decision making at national or continental scale. The scale references the larger **movement** distances undertaken for occasional dispersal and seasonal migration at **regional** and continental scales. See also **Landscape**	Chapters 3, 4 and 5
Biodiversity Forecasting Tool (BFT) (Chapter 2)	An environmental classification (usually vegetation communities) is used as a surrogate for biodiversity to evaluate biodiversity **persistence**. Persistence is (separately) modelled as the response to alternative management actions and integrates composition, condition, spatial context and representation within an analysis drawing on metapopulation theory. The management actions considered are typically (1) maintain current high vegetation condition, or (2) improve current vegetation condition (through infilling, buffering and revegetation). Generic maximum mobility parameters for landscape-scale faunal movement (typically 2000-5000 m) are estimated and aim to capture any species that might undertake nomadic and migratory movement at that scale. BFT uses a **cost–benefit approach least-cost paths** analysis to undertake the analysis of spatial configuration. A biodiversity index (BDI) is calculated which provides an evaluation of a region's capacity to support biodiversity at a given time. The changes in biodiversity index (referred to as **benefit**) from the original state to that arising from the management changes are calculated and mapped as Conservation Benefits. High benefit areas are where alternative management would provide greatest benefit in relation to the region's overall biodiversity.	
(Landscape) Connectivity	A widely used concept related to landscape change and central to discussions of **fragmentation**. In this study, the intent of connectivity is to facilitate **movement** of individuals across multiple scales. This can mean the rescue of small populations	Throughout thesis

(Chapter 1)	from local **extinction** while favouring the recolonisation of suitable habitats. When viewed from a behaviour-based perspective, connectivity is a characteristic of the **matrix** between subpopulations rather than a characteristic of patches or landscapes. Therefore, connectivity is defined as “the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure”. Movement depends not just on distances between subpopulations but on the physical characteristics of the matrix itself, particularly the presence of habitat elements too small for settlement but which might nonetheless facilitate movement. Two types of connectivity are described: structural connectivity and functional connectivity. **Structural connectivity** is based on physical landscape elements such as patches, **corridors** and **stepping stones**, and does not consider behavioural responses of an organism to landscape structure. It may also be described as the physical characteristics of the landscape between patches of occupied habitat. **Functional connectivity** considers the behavioural response of an organism (such as dispersal capacity) to individual landscape elements and the element’s spatial configuration. Structural connectivity can contribute significantly to functional connectivity (but structural connectivity does not guarantee functional connectivity). There are two categories of functional connectivity: **potential** and **actual.** Potential connectivity combines physical attributes of the landscape with estimates of dispersal ability to predict the species-specific level of landscape connectedness. Actual connectivity extends potential connectivity by combining physical attributes with observed dispersal between patches or through the landscape. See also **Landscape connectivity**	
(Wildlife) Corridor (Chapter 1)	Corridors, usually linear features, can be contiguous stretches of habitat connecting larger habitat patches or composed of **stepping stones**. Corridors may also occur between non-linear arrangements of habitat fragments where the gaps provide limited **permeability** for species movement. Corridors can be established at different scales, e.g. **regional**, national or **local**. At regional and national level ecological corridors refer to continuous habitat stretches (such as river valleys and water courses) and/or mosaic of habitat types that allow movement of species within the landscape. At local level corridors can consist of landscape elements such as hedgerows, dikes and road verges. It is to be noted that the proper scale of implementation is to a large extent species dependent and these aspects should be, therefore, taken into consideration. (13)	Chapters 2, 3 and 5
Cost (of movement) (Chapter 2)	The ease or energy cost to the individual of traversing the landscape; or the (inverse of) likelihood of successful movement. The cost (**permeability**) grid records the ease of **movement** across the region, that is, if habitat impedes the mobility of a species it is costing the organism more effort to permeate through it and it is less likely to be successful than would be the case in an ideal habitat. (2) See also **Cost–benefit approach**; **Least-cost paths**	Chapter 3
Cost–benefit approach (CBA) (Chapter 2)	A modelling approach that integrates the cost of movement for organisms with the benefits of access to habitat across a variegated landscape. Using raster grids, and a **least-cost paths** analysis, it models spatial context of each site (cell). That is, it models the landscape context of each site (referred to as its **neighbourhood habitat value**) from the perspective of a species home range requirements and dispersal abilities to determine the site’s connectivity to other habitat. In so doing, it	Chapter 3

	integrates the amount of habitat, its condition and level of fragmentation for every grid cell across the landscape. (2) Habitat is represented as a benefit grid (indicating **habitat suitability**) while the resistance to movement through the landscape is represented by a **cost** grid.	
Ecological network (Chapter 1)	A coherent system of natural and/or semi-natural landscape elements that is configured and managed with the objective of maintaining or restoring ecological functions as a means to conserve biodiversity while also providing appropriate opportunities for the sustainable use of natural resources. (13) In this study, several types of networks are discussed: connectivity network, dispersal network and habitat network.	Chapters 2 and 3
Enhanced regional connectivity (Chapter 2)	**Regional-scale connectivity** was integrated with the broad-scale (NSW state) **NVMBA Landscape value (LV)** layer to enhance regional-scale connectivity. As both regional connectivity and LV originated from additive processes within the **SLT**, both inputs were combined by adding their respective values at each location with equal weighting. This enhancement identified, within the LV zones, habitat patches not included in the broad-scale analysis and placed smaller-scale faunal movements for daily foraging and local dispersal within the context of the larger spatial and temporal scales appropriate for migration, inter-generational **dispersal** and long-term **persistence**. Management in this zone should aim to retain existing links or consolidate links by extending existing habitat patches, or revegetating to reduce the isolation of remnants. See also **Movement**	Chapter 5 (for simplicity this is referred to as regional connectivity in this chapter)
Extinction (Chapter 1)	The complete disappearance of an entire species. Extinction can occur across different spatial scales. Local extinctions of small populations in insular habitats are common events for a diverse range of taxa. In most cases local extinctions can be countered by recolonisation of the area from a larger 'mainland' population. (13) See also **Metapopulation persistence**	
Extinction debt (Chapter 1)	The future extinction of species due to past events, such as habitat loss. Extinction may still occur even if no further habitat loss occurs as current resources may be insufficient to maintain the species. May also be used to describe the process of faunal decline in fragmented landscapes where sub-populations are lost at a greater rate than new remnants are colonised until the whole **metapopulation** goes extinct. (5)	Chapter 4
Focal species approach (Chapter 1)	A focal species approach is a multi-species approach for managing against a threat. Focal species have been identified as having similar habitat requirements and responses, and similar sensitivity to an identified threat such as **fragmentation**. It is argued that tailoring management options to minimise the threat to these most sensitive species will cater for those species which are less affected by the threat. The approach differs from the umbrella species concept, and flagship and indicator species approaches by using the threatening process to select the focal species and uses multiple species compared to a single species. (12,14)	

	See also **Generic focal species**	
Fragmentation (Chapter 1)	Fragmentation is a poorly defined or inconsistently used term. (15) Two process act to effect habitat change: a) habitat loss - the loss of species' natural habitat, and b) habitat fragmentation *per se* - the creation of smaller, isolated remnant habitat patches through the process of breaking apart of continuous habitat. (3) These are landscape-scale processes, which can change ecological processes, the spatial patterns of vegetation cover, and influence individual species and assemblages. (15) The two processes often work in parallel and the term 'landscape change' has been suggested as a clearer alternative. (1) In this study, fragmentation' has been used throughout to describe the landscape change investigated by the various analyses. See also **Connectivity**	Throughout thesis
Functional connectivity (Chapter 1)	See **Connectivity**	Chapter 5
Generic focal species (GFS) (Chapter 1)	The GFS approach extends the **focal species approach** but the GFS is not an existing species. Rather, the approach combines multiple characteristics of a group of species, sensitive to a particular threat, into a virtual species. The approach was not designed to represent a single existing species as it would be unrealistic to expect one species to exhibit the range full range of characteristics of the group. The GFS utilises threat-sensitive, real species to enable an evaluation of how well a landscape would support a broader range of species, thus alleviating the need to parameterise and run many individual models.	Chapters 3, 4 and 5
Graph theory (Chapters 1)	The graph-theoretic approach represents the connectivity of a set of habitat patches as a "habitat graph," a collection of nodes (habitat patches) and **links** that connect pairs of nodes (representing the potential or frequency of **movement** between habitat patches). The way in which nodes and links are defined will determine whether the habitat graph represents **structural**, **potential** or **functional connectivity** among habitat patches. (18)	Chapter 2
Habitat suitability (Chapter 2)	As applied in the **REMP** models for this study, habitat suitability refers to every combination of land use and vegetation formation. This information is used to assign an individual habitat value (i.e. **habitat suitability** for the species of interest) to each grid cell (19). It is an indication of the quality of the habitat under varying land uses. In this study, these values for the **generic focal species** and any individual species were determined previously from expert elicitation.	Chapters 3 and 4
Local scale (Chapter 2)	In this study, local scale approximated a single field or farm (i.e. from several hectares to hundreds of hectares), which is the level at which restoration activities are planned, implemented and paid for in the study region. It references smaller **movement** distances such as day-to-day foraging. See also **Landscape**	Chapter 5

Landscape (Chapter 1)	Definitions of landscape are numerous but usually contain reference to the elements found within (such as patches) and their heterogeneous nature. It may be viewed as 1) a level belonging to an ecological hierarchy ("landscape level"), covering greater variety than individual habitats, and 2) a spatial scale of resolution corresponding to human perceptions, usually varying from hectares to kilometres. Both views are dependent upon the scale of observation and the research question. The relevance of the concept of landscape, however, is how ecological phenomena (e.g. population dynamics and species movement) are manifest. In this study, reference to landscapes are at the local, regional and state scale, and acknowledge this division encompasses both human perceptions and realised scales of ecological phenomena. (7, 20) See also **Broad scale**; **Local scale**; **Regional scale**	Throughout thesis
Landscape ecology (Chapter 1)	Emphasises how the characteristics and structure of the **landscape** as a whole affects the **movement** of populations, disturbances (human and natural) and materials, with the result that a connected landscape facilitates movement from one location to another. See also **Metapopulation theory**	Throughout thesis
Landscape connectivity (Chapter 1)	The relationship between an organism and its environment; it conceptualises the dependence of species dispersal on landscape structure and **matrix** features, and is best viewed from a species-centric perspective. See also **Connectivity**; **Movement**	Throughout thesis
Landscape capacity (Chapter 3)	See also **Metapopulation capacity**	Chapters 4 and 5
Landscape value (LV) (Chapter 2)	An indicator of the spatial context of the structural elements in the landscape – how well a site is connected to other habitat sites, and how well the site contributes, by virtue of its landscape position, to habitat connectivity of other sites. LV uses **cost–benefit approach** and s**patial links tool** to calculate cross-scale **connectivity** based on habitat configuration and condition, and species movement distances. LV concentrates on identifying linkages that are appropriate for day-to-day movements, as well as dispersal, migration and potential climate-induced range shifts. Estimated movement distances ranged from 31.25 km to 500 km. The LV **links** represent zones where wider-ranging mobility is feasible but where localised actions such as revegetation could be undertaken to increase the potential for daily movement. See also **Movement**	Chapter 5
Least-cost paths (Chapter 2)	Computer algorithm which find the least costly (or optimal) path for animal **movement** between patches or points on the landscape based on movement abilities and habitat preferences. Paths are based on resistance (or **cost**) maps reflecting the difficulty for a species to move between two sources. A species accumulates a cost with increasing distance from its source, depending on its dispersal capacities and specific habitat encountered.	

	See also **Cost–benefit approach**; **Graph theory**	
Link (Chapter 2)	Part of the **landscape** that facilitates connectivity between habitat patches. In **spatial links tool**, the length and strength of a link is related to the amount of habitat at either end of the link and to the resistance to movement of the intervening landscape. Calculation of a link requires **habitat suitability** values for the source and destination cells of the **least-cost path** and an average dispersal distance of the fauna concerned. See also **Movement**; S**patial links tool**	Chapters 3, 4 and 5
Local-scale connectivity (Chapter 2)	Captures movement at the scale of daily forays for food and other resources and dispersal. Local-scale **connectivity** was calculated using the **cost–benefit approach** and the **spatial links tool** for defining neighbourhood context. Connectivity was based on estimated patch size preference and movement distances for woodland birds. The final product was layer of 1.1 km links situated between 10-ha patches set amongst the <100-m gaps in woody canopy cover. See also **Movement**	
Matrix (Chapter 1)	The areas of the landscape outside patches of suitable habitat. The matrix may range from areas of similar vegetation structure and composition to the species' suitable habitat through to anthropogenic land uses that replace cleared habitat. Different matrices vary in the extent to which they supply substitute resources or impede dispersal. See also **Movement**	Chapters 3 and 5
Metapopulation (Chapter 1)	The term was introduced by Richard Levins in 1969 and marked the beginning of contemporary metapopulation studies. (6) His original definition (a 'population of populations') has been refined to 'a set of discrete populations of the same species in the same general geographical area that may exchange individuals through migration, dispersal, or human-mediated movement.'	Throughout thesis
Metapopulation Capacity (MPC) (Chapter 3)	The persistence of a metapopulation depends on the metapopulation capacity of the fragmented **landscape**. (9, 10). Derived from **metapopulation theory**, the regional MPC is a single value that describes the ability of a region to support a viable population and it is determined by the quantity and spatial distribution of habitat in relation to each species' habitat requirements and **movement** abilities. Thus, it recognises that local population dynamics and connections among different habit patches vary across the landscape. (11) Single metapopulations are identified from cells having the same MPC value (a grid produced by **REMP**) and a region may have more than one metapopulation, each functionally distinct from the other. The single MPC value for the region represents the value for the most robust metapopulation. However, the remaining metapopulations provide an ecological insurance in the event of a stochastic event. The landscape's capacity to support a viable metapopulation is determined from the comparison of the MPC value of the most robust metapopulation with an extinction threshold calculated for MPC. This threshold is derived as the MPC of idealised habitat, in maximum condition, with an area equal to the minimum viable habitat (specified as one of the REMP parameters). A metapopulation will be viable, i.e., persist, if the MPC is greater than the extinction threshold, indicating that connected habitat exceeds the	Chapters 4 and 5

	required minimum. The MPC can be used to assess a current landscape or a landscape modified by land use change e.g. revegetation. (19)	
Metapopulation persistence (Chapter 1)	The ability of a population to maintain numbers or increase when rare. That is, when a population is small, the rate of species entering population (or patch) (colonisation) is greater than **extinction** rate. This describes a positive equilibrium. Local population dynamics primarily affects extinction while dispersal and **connectivity** primarily effect colonisation. The amount of available suitable habitat also affects overall population dynamics and persistence. (11) See also **Metapopulation capacity**; **Movement**	Throughout thesis
Metapopulation ecology (Chapter 1)	The field of ecology that studies the dynamics of fragmented populations in heterogeneous landscapes. **(13)** See also **Metapopulation**; **Metapopulation persistence**; **Metapopulation theory**	Throughout thesis
Metapopulation theory/Metapopulation approach (Chapter 1)	Metapopulation theory, put simply, deals with the notion of discrete local breeding populations connected by migration. (6) The metapopulation first suggested by Levin (see **Metapopulation**) assumed 1) a landscape of discrete patches of suitable habitat set among non-suitable habitat; 2) habitat patches are of equal (small) area and isolation; 3) local populations in the metapopulation have independent dynamics (e.g. extinction), and 4) the exchange of individual between local populations is low so that local dynamics occur at a faster rate compared to the metapopulation. (6) This last assumption implies a metapopulation in balance between local extinctions and establishment of new populations in unoccupied habitat. (7) However, these requirements are rarely, if ever, met. The theory later developed to consider population dynamics in highly fragmented landscapes and to integrate effects of patch area and isolation on species movement, extinction of populations and establishment of new populations at empty sites. (7)	Throughout thesis
Movement (Chapter 1)	The ability of an organism to travel through the landscape mosaic and is a function of landscape **permeability**, **connectivity** and the individual movement characteristics of the individual or species. (13) Examples include daily foraging excursions from resident habitat for resources, dispersing (emigrating) to a new habitat patch and seasonal long-distance migration. Hence, the scale of movement is critical for discussions on **connectivity**.	Throughout thesis
Native Vegetation Management Benefit Analysis (NVMBA) (Chapter 2):	The analysis predicts where native vegetation management will contribute highest **benefit** to terrestrial biodiversity at a state scale. The analyses focus on improving the condition, extent and connectivity of vegetation formations. NVMBA consists of two modules, the **Biodiversity Forecasting Tool** (BFT) and **Landscape Value (LV)**. Four Benefit zones comprise NVMBA: • From BFT o ‘Manage’ **benefits** are areas of existing native vegetation in good condition and where emphasis on	Chapter 5

	management would be on maintaining this high condition. o 'Improve' benefits also relate to areas of existing native vegetation, and while they are generally better examples of more heavily altered vegetation types, they nonetheless require some form of active management to improve their condition. o 'Revegetate' benefits are cleared areas where replanting or natural regeneration of species that previously occurred at the site would return the highest benefit. • From LV o 'Consolidate' **benefits** highlight areas where emphasis on linking, or retaining the current connectivity values of core remnants, would provide greatest benefit.	
Neighbourhood habitat value (Chapter 2)	Based on the concept of "habitat neighbourhood" sometimes employed in **metapopulation ecology**, in which the amount of habitat "available" to an individual animal or plant at a given locality is calculated as a function of the size of the habitat patches in the surrounding neighbourhood and the isolation (or, inversely, connectedness) of these patches relative to the locality of interest. Neighbourhood habitat value extends the habitat neighbourhood approach to work with grid-cell data, rather than polygonal data, and with continuous measures of habitat suitability or condition, rather than a simple suitable/unsuitable habitat classification. (17)	Chapter 3
Permeability (Chapter 1)	The extent to which the elements of the entire landscape either allow or encourage animal **movement** through the landscape. It considers the contribution of the **matrix** to movement in addition to structural **connectivity**. (13) In this study, permeability is a property of both individual grid-cells and the whole dispersal paths. See also **Cost**	Chapters 2 and 3
Persistence	See **Metapopulation persistence**	
Regional scale (Chapter 2)	**A**pproximates the scale of the NRM agencies' planning, investment and administration (i.e. from 10^4–10^7 ha). It references the larger **movement** distances undertaken for occasional dispersal and seasonal migration. See also **Broad scale**; **Landscape**	Chapter 3 and 5
Regional connectivity (Chapter 2)	An interim step towards integrating the local- and broad-scale components and focussed on intermediate-scale faunal movement. Regional **links** were calculated using the **spatial links tool** with a maximum link length of 2.5 km specified. This extended the 1.1-km dispersal distance used in the **local-scale connectivity** analysis to include the pathway that a woodland species may take on rare longer-distance excursions for foraging as well as for dispersal between subpopulations. See also **Movement**	see **Enhanced regional connectivity** in reference to Chapter 5

Rapid Evaluation of Metapopulation Persistence (REMP) (Chapter 3)	REMP is a spatial modelling tool that employs a species-focused approach in assessing landscape **fragmentation** by integrating biological processes with variegated landscape habitat patterns, using continuous grid surfaces. REMP produces a predictive map of persistent **metapopulation(s)** and a **metapopulation capacity** value for the landscape.	Chapters 4 and 5
Spatial links tool (SLT) (Chapter 2)	Models links between habitat sites with good spatial context. SLT produces a map of **link value** across a region by combining **connectivity** measures from **metapopulation ecology** with the **least-cost paths** algorithm from **graph theory**. Link value is defined as the contribution that a site makes to **landscape connectivity** by contributing to the connectivity between other sites. The SLT identifies ecologically efficient paths in proportion to the amount of habitat at either end of any given link, ignoring habitat features that do not play a role in connecting habitat. It does not delineate corridors.	Chapter 3
Stepping stone (Chapter 1)	An ecological **corridor** formed by non-linearly connected resource/habitat patches that allow organisms to disperse between the patches (e.g. core areas within an ecological network). (13) See also **Ecological network**; **Movement**	Chapters 2 and 5
Structural connectivity (Chapter 1)	See **Connectivity**	Chapters 2 and 5
Time lag (Chapter 4)	The time taken for a species, population or **metapopulations** to respond to landscape changes. Current species distribution and current **landscape** pattern should not be assumed to be directly related; current distributions may also reflect past landscape conditions. Time delays are important because they may determine how much extinction is ahead. (16)	Chapter 4

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